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AN ECOLOGICAL STUDY OF THE DERMAPTERA AND ORTHOPTERA OF THE WELAKA AREA IN NORTHERN FLORIDA

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INTRODUCTION

The insects of the Order Orthoptera are among the more abundant and conspicuous invertebrate inhabitants of terrestrial environments in the temperate and tropical regions. We find that American students of the group have been concerned chiefly with taxonomic studies, regional lists and detailed investigations of individual species, generally those of economic importance. The contributions to our knowledge of the life histories, behavior, and ecology of these insects are contrastingly meagre, and only in recent years have many studies been especially focused on these aspects of orthopteran biology.

In general, those ecological investigations which have been conducted in North America have dealt largely with the faunas of mid-northern, northwestern, mid-western, and southwestern regions. The southeastern United States seems to have been particularly neglected from the standpoint of detailed ecological studies, and it was largely due to this fact that the present study was undertaken.

The study presented in the following pages is an attempt to show the ecological relationships of the Orthoptera inhabiting a limited area in Florida, a state in which there is a far richer fauna of these insects than in any other in North America, and in which there occur the most diverse habitats and varied environmental relationships. Fifteen months were spent in almost daily observation and collection of the Orthoptera within the University of Florida Conservation Reserve, a tract of over 2,000 acres near the small town of Welaka on the east shore of the St. Johns River in northeastern Florida. While much remains to be done, it is my hope that this paper may serve as a guide and aid for similar investigations in other parts of Florida and the southeastern coastal plain generally. If it serves to emphasize how much remains to be learned about our Floridian fauna, and what a wide and fascinating field of study here lies open to the ecologist, its purposes will have been served.

Two main objectives were kept foremost in mind in the planning and carrying out of the problems; first, to determine just what species were present in the Welaka area and, secondly, to discover what environments they occupied and to work out a classification of the orthopteran habitats based upon the occurrence and ecological relationships of the insects themselves. This latter endeavor led to the recognition of a number of orthopteran assemblages living in habi-

tats characterized principally by their plant associations and secondarily by their soil and water relations. The attempt was made, with some degree of success, to establish correlations between the presence or absence of particular species or species assemblages with the general characteristics of these habitats, and so far as possible with the specific features or elements of them.

Many interesting problems other than ecological presented themselves during the course of this investigation and lured me into paths which, in some instances, deviated far from the main objectives. To have followed all of these to their conclusion would have extended the investigation indefinitely; limitations of time and energy made it impossible to devote much attention to the study of life histories, local variation, predators and parasites, behavior including songs and mating habits, and a host of other points that bear to some degree upon the ecological problem. A portion of the information gathered concerning these matters, where it is not too inconclusive or fragmentary, is to be presented elsewhere in other publications.

The taxonomic status of certain of the species living on the reserve presented problems of interest which require elucidation. One of the larger grasshoppers proved to be an undescribed species or subspecies related to *Melanoplus furcatus* Scudder. It is a member of the very plastic Clypeatus Group which is confined to southern Georgia and northern Florida, and which presents a complex of species and subspecies that needs much further study for their interpretation. Dr. T. H. Hubbell of the Museum of Zoology, University of Michigan, is now working on such a study. In the instance of the cockroach *Cariblatta lutea* (S. & Z.) no difficulty was found in assigning Welaka material to one or the other of the two presumptive races *lutea* and *minima*. Their overlapping distribution in this area without seeming to intergrade makes me question their status of geographical races in the accepted sense. This problem is now being investigated more fully. From the study of the two polytypic species *Aptenopedes aptera* Scudder and *Aptenopedes sphenarioides* Scudder, in Florida generally, as well as in the Welaka area, it has become apparent that much more remains to be learned about these peculiar endemic forms. A thorough taxonomic study based upon all available material, supplemented by the results of additional collecting in little-worked areas, will be required to untangle the complexities of their specific and racial relationships and distribution.

ACKNOWLEDGMENTS

In the pursuance of this problem I have been assisted by many individuals in many ways. I wish to express my sincere gratitude to Dr. J. S. Rogers and Dr. T. H. Hubbell, formerly of the Biology Department of the University of Florida and who are now Director and Curator of the Division of Insects, respectively, of the Museum of Zoology, University of Michigan. Dr. Hubbell has given advice and encouragement throughout the course of the study and has identified many of the specimens collected, and he has also checked my own determinations, and has given much of his time to the correction and criticism of the manuscript. Dr. Rogers made it possible to carry on the work at the Welaka reserve by his assistance in securing funds, and he has given many valuable suggestions and criticisms. To Dr. H. B. Sherman of the Department of Biology, University of Florida, I am grateful for his help in obtaining a set of aerial photographs of the University of Florida Conservation Reserve, and for the work he did in connection with the mapping of the area.

I wish to express my deep appreciation to Frederick M. Gaige, former director of the Museum of Zoology, University of Michigan, for financial assistance and the constant interest in this study. He also made possible the use of the facilities and collections of that museum.

The field work was greatly facilitated and made more pleasant through the interest and cooperation of the superintendent of the reserve, Mr. William M. Dunson. Mr. Root, the former resident forester, aided in making and securing equipment, in preparing maps and by bringing many specimens to me from the field.

Many other persons at the University of Florida helped in ways too numerous to mention, and to each I am obligated in one way or another. Dr. Albert M. Laessle, who was a colleague on the reserve, was especially helpful. The results of his study on the plant habitats of this area (1942) have furnished much of the basis for the vegetational scheme of classification for the orthopteran habitats which I adopted, and his aid in determining the plants of the region has been of inestimable value. I am also indebted to Mr. Joseph C. Moore, also a fellow worker on the reserve, for the excellent map which he made.

The final preparation of the manuscript was made with the diligent help of my wife, Frances C. Friauf, and her steadfast encouragement throughout the study has made its completion possible.

LITERATURE RELATING TO THE PROBLEM

Works covering the more general aspects of the problems of ecology in the Orthoptera are by Chopard (1938) and Uvarov (1928). The former is a comprehensive summary of ecological factors, but little attention is given to local habitat relationships, and it is based largely on the Old World fauna. The latter work includes much ecological data on the Acrididae, and it is especially valuable because it points out problems that need study. While the generalizations in this book may be of universal application, the specific treatments again are confined to the extra-North American fauna. Many other investigators in the Old World, before the war, were active in this field, and they have contributed detailed ecological studies of merit.

Those ecological investigations which have been

conducted in North America have dealt with faunas outside of Florida. Among the more important investigations of this class are the following: Shull (1911), Hancock (1911), Vestal (1913), Buckell (1921), Hubbell (1922), Strohecker (1937), Isely (1937, 1938), Fulton's several works on the ecology and life histories of some of the Gryllidae (1915, 1926, 1931), Knutson (1940), Urquhart (1941), and Cantrall (1943). The last study mentioned is the only one which is entirely comparable to that here presented. I had more or less intimate contact with his investigation from the beginning, and I adopted some of the methods he used.

For the southeastern United States, the following are the more important contributions which deal directly or indirectly with the ecology of Orthoptera. Blatchley's work on the northeastern American Orthoptera (1920) contains descriptions of most of the species here considered, and some information is given concerning their distribution, life histories, habits, and habitats. Morse's two volumes (1904, 1907) are of particular interest to the ecologist because of the classification of orthopteran associations which he proposed. They also treat specifically of much of the fauna of northern Florida and of neighboring regions, and they give valuable information on the habitats and distribution of the various acridid species. Another basic work is that of Rehn & Hebard (1916). This is practically indispensable for any worker in northern Florida because of the zonal classifications and relationships therein proposed, the detailed taxonomic summaries of the species treated, and for the many notes on distribution, habits, and habitats. Fox's papers (1915, 1917) also have been extremely useful. While these papers are concerned with the broader zonal relationships between the Orthoptera and the regions covered, they furnish many clues to the development of local habitat associations and species assemblages. The Virginia paper is of special interest in regard to north Florida Orthoptera because of its ecological, distributional, and life history notes on the large number of species common to both regions.

It hardly seems necessary to point out the need for thorough investigations in the physiology, genetics, embryology and post-embryonic development of the species in this group of insects as necessary adjuncts to ecological work. By such studies we are better able to determine the basis for the correlations between the fauna and certain factors of the environment. One cannot turn to one or two sources for the information which has been accumulated on these phases of orthopteran biology. It is scattered through countless journals, pamphlets, papers, and books written in several languages. Two volumes which do contain a large amount of this material are those of Uvarov and Chopard previously mentioned. Among the most important contributions to these fields in this country, and whose contributions should be turned to in connection with these problems, are those of Carothers, Bodine, King, Slifer, Nabours, Criddle, and Yeager.

THE AREA OF STUDY

LOCATION

The University of Florida Conservation Reserve is a tract of land approximately 2180 acres in extent along the St. Johns River in the central portion of Range 26 east, Township 12 south, Putnam County, Florida. The northern boundary is practically coincident with the southern limits of the little town of Welaka, and from this line the reserve extends south for a distance of about two and one-half miles. Its western boundary is formed by the irregular shoreline of the St. Johns River, and the eastern boundary lies from one and one-half to two miles distant from the river (Figs. 1 and 2).

This investigation was carried on entirely within the confines of the reserve, with the following three notable exceptions: (1) since the Scrub Habitat is represented on the reserve only by a small area which is continuous with a larger tract along Beecher Spring Run, immediately south of the reserve boundary, much of the collecting in this habitat was done in the more extensive area; (2) studies of the Scrub Habitat were also extended to a very large strip of

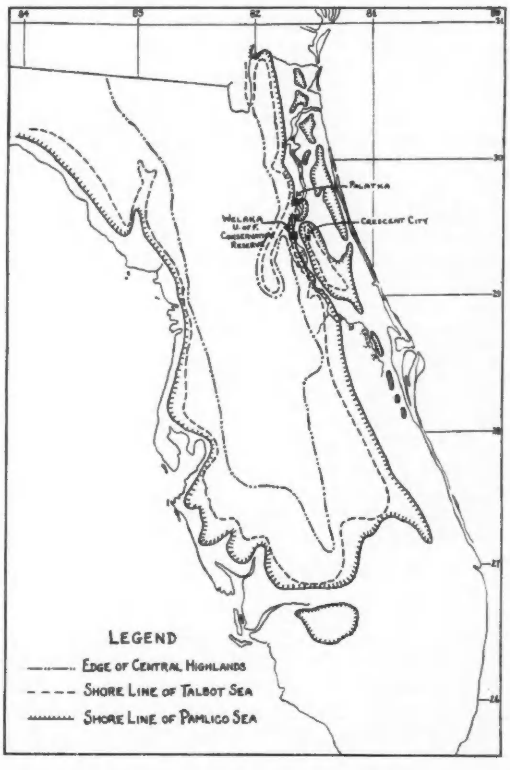


FIG. 1. Outline map of peninsular Florida, showing the location of the University of Florida Conservation Reserve and the positions of the Pleistocene shore lines which are of importance for the Welaka area. (Modified from Cooke 1939.)

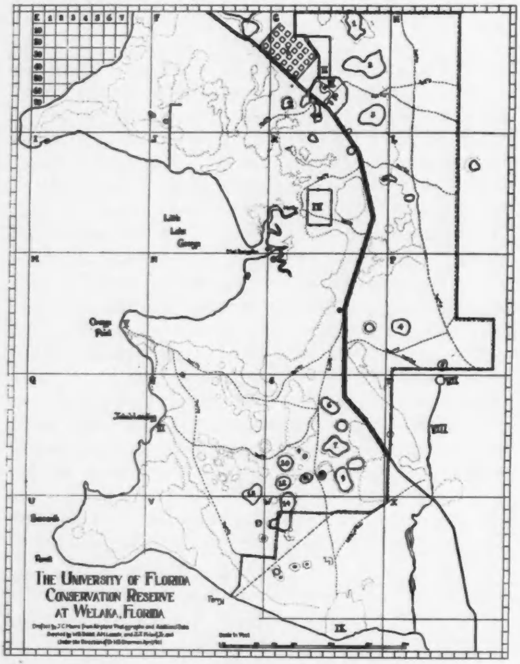


FIG. 2. Map of the University of Florida Conservation Reserve, Welaka, Florida, showing the method in which the reserve was cross-sectioned for the purpose of locating positions and collecting stations. I, fish hatchery ponds; II, new quail hatchery; III, administration grounds; IV, old quail hatchery; V, shell mound at Orange Point; VI, shell mound at John's Landing; VII, Beecher Springs; VIII, Beecher Spring Run; IX, Mount Royal. The flatwoods ponds which were studied are indicated by the numbers 1-15.

this habitat situated 2.3 miles west of Huntington along the road which leads from Crescent City to the Welaka-Georgetown road; (3) a pond, approximately one mile southeast of the southeast corner of the reserve, was also included as a collecting station since it is the nearest pond which has any considerable amount of guinea cypress (*Hypericum*) growing around its margin. None of the ponds within the reserve have more than a few marginal bushes of this plant (the food-plant of *Inscudderia strigata* (Scudder)).

HISTORY

Stretching back unnumbered generations into the past, the aboriginal Indian tribes inhabited small settlements all up and down the St. Johns River. Here they hunted in the virgin and primeval pine lands and hammocks and swamps of sub-tropical splendor; they also fished in this largest of Florida rivers and gathered the fresh-water snails (mainly *Viviparus* and *Ampullaria*) which formed a large part of their diet. The shells of these were thrown into midden heaps which mark for posterity the record of human occupancy of the dwelling sites. Two such shell mounds are to be found on the reserve, one on the tip of Orange Point and another just south of John's Landing. Both of these mounds, like many others in Florida, have suffered from the ravages of the road-builders. Very recently they have been more completely destroyed to build many of the trails upon the reserve itself.

Exactly what the Welaka area was like when the Indians lived there can only be guessed. In general aspects it was probably little different from today, but the big pines which dominated the flatwoods are gone and the giant cypresses no longer stand majestic in the river swamps.

The early Spanish settlers also have left their mark upon the reserve. A large rice plantation occupied much of the tract which is now *Spartina* marsh on Buzzard's Roost Point, and they undoubtedly cut some of the virgin timber in this area.

In 1765-66 John Bartram, and in 1775 William Bartram, his son, traveled up the St. Johns River and stopped at several spots in this area. One such place, which John named Mount Hope, may have been Orange Point or the neck of land jutting out into the north end of Little Lake George. Mount Royal, which lies just south and east of the southern boundary of the reserve, is mentioned several times in the diaries of both of these Quaker naturalists. A fairly good idea of what the vegetational aspects of this region were like two centuries ago can be gleaned from their journals. That William actually set foot on the southern part of the area now within the confines of the reserve is not to be doubted, for he describes clearly his tracing of the ceremonial ramp which leads to a large Indian mound at Mount Royal. This ramp can be seen even to this day extending to the border of the southernmost pond in the southeastern part of the reserve just east of trail 4. He has written as follows in his "Travels," reminiscing on the aspect and change that had occurred since his first view of this place some fifteen years previously: "The glittering water pond played on the sight, through the dark grove, like a brilliant diamond, on the bosom of the illumined savanna, bordered with various flowery shrubs and plants; and as we advanced onto the plain, the sight was agreeably relieved by a distant view of the forest, which partly environed the green expanse of the left hand, whilest the imagination was still flattered and entertained by the far distant misty points of the surrounding forests, which projected into the plain, alternately appearing and disappearing, making a grand sweep around on the right, to the distant banks of the great lake (Lake George). But that venerable grove is now no more (a live oak grove which surrounded Mount Royal, and which still stands as a remnant). All has been cleared away and planted with indigo, corn, and cotton, but since deserted; there was now scarcely five acres of ground under fence. It appeared like a desert to a great extent, and terminated, on the land side, by frightful thick-

ets, and open pine forests." These open pine forests are still the conspicuous feature of the area in this southeastern corner of the reserve.

There was probably intermittent residence upon the reserve immediately along the river at Orange Point, John's Landing, and certainly at Mount Royal from the time of the Bartrams down to times within the memory of the present inhabitants of this region. The residents must have cultivated small tracts of land surrounding these places, and probably cut numbers of the trees. Some years previous to 1899, an Englishman cleared a considerable part of the land on Orange Point and turned it into an orange grove, planting a part of it to indigo. The hard freeze of 1899 killed many of his trees, and he finally abandoned this location. The effects of this clearing are still evident; much of what would otherwise be an extensive xeric or live oak hammock is now partly open weed growth or has grown up into a second growth of shrubs and small trees. The orange trees are still standing, and the indigo has spread to many parts of the still open grassland. Another residence was also established at John's Landing not long afterwards, and a large field was there put under cultivation. Here, too, a large part of the xeric hammock land was cleared and is now covered with shrubs and small tree growth. This site has been abandoned only very recently, and the structures which stood there have been torn down within the past seven years.

During the latter part of the last and the early part of this century, practically all of the virgin longleaf and slash pines were cut in all of the Welaka area, and the large and valuable cypress trees in the swamps fell under the lumberman's axe. A large part of the second growth pines have since been heavily turpentined.

In 1935, the area which is now the University of Florida Conservation Reserve was taken over by the United States Government as a Transient Camp under the Resettlement Administration. From 1935 until 1938, when it came under the jurisdiction of the University of Florida, a large number of inroads were made into the natural conditions of the reserve. The second growth pines from some areas were cut, and in other areas a reforestation project was established; over a large part of the flatwoods a forest stand improvement program was inaugurated, the underbrush, herbaceous growth, and fallen logs being cleared away; the present trails which ramify through the reserve were built and fire breaks were made; the land just to the east of Mud Springs was cleared and a small quail hatchery was built; and in the northwestern corner of the reserve a large tract of flatwoods was cleared for a proposed airport.

Since 1938, and during the time this investigation was carried on, little was done to alter the biotic and physiographic relationships of the reserve. The fire lanes were maintained and were plowed in the late fall; the roads and trails are kept passable and a wire fence has been placed completely around the boundary line. The area is used by both the Forestry School and the Biology Department of the University. In collaboration, these two departments have established certain areas which are to be maintained inviolate for biological studies. Recently, the Forestry School has been cutting out a large amount of marked timber, mostly slash pine and longleaf pine which has been heavily turpentined.

It would be of much interest to reexamine the orthopteran populations and habitats at some future time for comparison with the results of the present study in order to determine what changes had been brought about in this area by successional influences in the plant associations. The inviolate biological tracts should be especially interesting in this regard.

ZONAL RELATIONS OF THE BIOTA

With respect to life-zones, northeastern Florida falls within the humid division of the Lower Austral Zone known as the Austroriparian (Louisianian) Division in terms of Merriam's Life Zones (1898), or as the Austroriparian Biotic Province according to Dice (1943). This division takes in the entire Southeastern Coastal Plain. Florida, along with the southern part of Alabama, Mississippi, and Louisiana, has sometimes been set off as a part of the "Gulf Strip" of this division in papers dealing with the zonal distribution of mammals (Howell 1921).

Upon the basis of orthopteran evidence, Rehn and Hebard (1916) divided the Costal Plain into two physiographic regions, the Upper and Lower Coastal Regions, Florida being included in the latter. In regard to life zones, they restricted the Austroriparian to the Upper Coastal Plain; co-extensive with the other physiographic division, the Lower Coastal Plain, they recognized a new life zone which they called the Basic Austral or Sabalian. This zone is characterized by a considerable number of species which extend as far south as southern or at least central and north-central Florida. It is to be realized, however, that no large part of the orthopteran fauna is confined to the limits of this classification. This divisional delimitation which Rehn and Hebard have proposed has been accepted in part outside of the field of entomology by some mammalogists and others.

Vegetationally, the Welaka area lies on the eastern edge of the district designated by Harper (1914) as the Peninsular Lake Region. In reality it is in a transitional zone between this region and that which he designated as the East Florida Flatwoods. The Peninsular Lake Region is characterized by several vegetational types. The uplands, where the soil is derived from sands other than dune materials, are covered for the most part with "high pine." On the uplands which represent old dunes, a typical vegetation known as sand scrub is dominant. The level areas are covered with flatwoods vegetation which scarcely differs from that of other regions, except that many of the flatwoods which occur along the Oklawaha and St. Johns Rivers have a vegetation which seems to be indicative of marl near the surface. Near streams and lakes one may find high hammocks on the more elevated areas, and the streams and lakes are often

bordered by non-alluvial swamps and peat prairies or marshes.

These vegetational characteristics which are well-marked in the Peninsular Lake Region are rather poorly represented and disconnected in the Welaka area. On most of the uplands, which are at a considerable distance from the river, one finds "high pine" on soil which has not originated from sand dunes, but such areas are all of comparatively small extent. On dune sand materials, the uplands are covered with sand scrub vegetation, but this scrub is not quite the same as that found in the large areas of this vegetational type in the Peninsular Lake Region. Its atypical nature is manifested, for example, by the absence, in many cases, of the typical rosemary shrub, *Ceratiola ericoides* Michx. Also, the sand pines do not form as characteristic a feature of the scrub in the Welaka region as they do in that which is more typical on the western side of the St. Johns River. The scrub areas in the Welaka region are all comparatively small in extent. The high hammocks are also poorly represented and are confined mostly to the immediate vicinity of the numerous spring heads found on higher ground along the St. Johns River. Even these are not typical and differ in many respects from the high hammocks of the Peninsular Lake Region. While, for the most part, one finds non-alluvial hammocks bordering the streams and lakes in the Peninsular Lake Region, in the Welaka area both non-alluvial and alluvial swamps are present along the St. Johns River.

In summary, while many of the vegetational types which characterize the Peninsular Lake Region are to be found in the Welaka area, they are outliers of these types. They are usually small and disconnected, and are not typical as judged by comparison with corresponding types in the region west of the St. Johns River.

The extensive level areas on the reserve, and, for the most part, all along the St. Johns River are occupied largely by a flatwoods vegetation which seems to correspond more closely with the type of flatwoods characteristic of the East Florida Flatwoods Region than with those of the Peninsular Lake Region. Harper describes the flatwoods of the former as "open forests of long-leaf pine, with an undergrowth of saw-palmetto, gallberry, wire-grass, etc., and bearing the marks of frequent fires . . . ." Among other characters of the East Florida Flatwoods are the "treeless marshes" which occur along the St. Johns River, and the presence of numerous shallow ponds and bays. A number of extensive areas of marsh are found within the reserve, and the shallow ponds and bays are a conspicuous feature of the landscape.

CLIMATE

In-so-far as the general climatic conditions directly or indirectly affect the distribution of the orthopteran species and communities, I wish to point out the salient features of the climate of the region studied. No detailed microclimatic analyses were made in the habitats in this study, but the general features of humidity, soil water, and temperature with relation to vegetational cover were taken into consideration in the classification of the habitats.

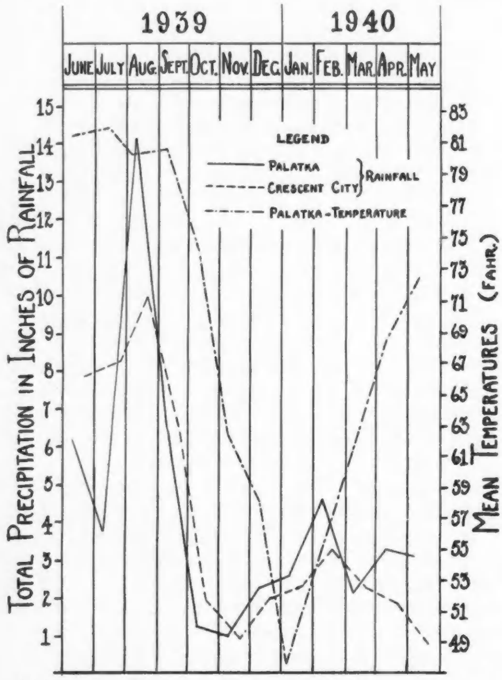
Because of its position between the Atlantic Ocean and the Gulf of Mexico, the average annual temperature of any section of Florida is rather uniform over a number of years. In northern Florida the average annual temperature is about 70 degrees Fahr. The four summer months of June, July, August, and September are very warm, with temperatures averaging 80-81 degrees. Killing frosts are likely to occur from the first week in November until the last of February, and occasionally they may occur as late as mid-April. Cold waves are usually of short duration, and freezing temperatures rarely last more than three consecutive days.

The average annual rainfall of northern Florida is approximately 50 inches, with slightly more than half of this amount falling during the summer months, when monthly averages are from 5-10 inches; during the remainder of the months this average is from 2-4 inches. The rainfall during the summer is largely in the form of thunder showers in the afternoons. A slight secondary maximum of rainfall is noticeable during the months of December, January, and February. This period is preceded in November, and followed in April and the first part of May, by marked periods of relative dryness.

Such a climate, although warmer, is as seasonal as that of Michigan, and correlated with the annual climatic cycle there is a very definite seasonal change in the orthopteran fauna as well as a definite seasonal progression in the life histories of the species. The winter fauna is very poor in species and individuals as compared with the summer. The majority of the Orthoptera on the reserve first appear during March and April or in the late summer and fall. The appearance of those in the spring correspond with the return of warm weather after the relatively cool winter and with the spring dry period which is most favorable for nymphs, for they have less chance of falling to the attack of certain fungi. Those nymphs which hatch during the late summer show a very definite cessation in growth about the middle of November, or the onset of first frosts, and they usually pass through the winter in this state of arrested growth.

No climatological data are available for Welaka, but weather recording stations have been maintained at two places near this area, one at Crescent City, ten miles southeast, since 1896, and one at Palatka, twelve miles northeast, since 1922. Records from these stations were compiled to give an indication of the climatological data for the Welaka area itself. They indicate that the climate of the Welaka area is fairly typical of that of northern peninsular Florida in general.

Graph 1 shows the temperatures and rainfall for one year of the period work was done on the reserve. Previous to this time, in the early months of 1939, the temperatures were unusually high. Averages were higher in only three other records for February, and the maximum of 94 degrees during this month has



GRAPH 1. Total monthly precipitation and mean monthly temperatures for the Welaka area during the period from June, 1939 through May, 1940. Data taken from weather station records at Palatka and Crescent City, Florida.

been equalled only once and never exceeded. The early appearance of *Romalea microptera* (Beauvois) especially, and other species as well, was undoubtedly the result of this warm weather. The Lubberly-locust began appearing during the second week in March in most localities in northern Florida, when ordinarily nymphs begin to emerge about a month later. April, which is usually very dry, was exceedingly wet, with the rainfall 150% higher than normal. Work on the reserve was begun in July, 1939, and the average rainfall for this month, as well as for August, was well above the average, the August average being the third highest on record. The final four months of 1939 were relatively dry. The average temperatures for these months varied little from normal, but October was very noticeably warmer than usual during the first two weeks, while the latter part of November and the latter part of December were exceptionally cold.

The opening month of 1940 was historical for its severe cold. No records since they began in 1891 report a colder January. The mean for stations in northern Florida averaged about ten degrees below normal. In the Welaka area, temperatures reached as low as 16 degrees Fahr. during the last week of the month, and the lowest temperature recorded for the state was eight degrees Fahr. Temperatures below normal averages continued until the last part of May. The seven months' period of colder than normal weather, from November, 1939 through May, 1940 is unique in the annals of the weather bureau. Temperatures averaged 3.2 degrees below normal each month except December when they were 2.0 degrees below. February had the lowest temperatures since 1912. In March the lowest temperature at Welaka was 36 degrees, and freezing temperatures were recorded at many stations in northern Florida. The first part of April was warm, but cold again set in during the second week, and most stations in northern Florida reported the coldest April weather on record. It dropped to 37 degrees in the Welaka area. The coldest temperature for May was 45 degrees Fahr. but during the latter part of the month warmer weather returned, and the remainder of the months until the end of October, when work was stopped on the reserve, were about normal.

Like the temperatures, precipitation was somewhat below normal except in February when it was 30% higher than average. April, which is always very dry, was slightly below normal rainfall. In contrast to this, the month of June had higher than normal rainfall and the remainder of the months during which field work was carried on in this area were about normal.

These facts of rainfall and temperature had to be taken into consideration in connection with the seasonal succession of the various species. Undoubtedly, because of the severely cold weather during the first months of the year 1940, the appearance of juveniles was somewhat later than usual, probably from two weeks to a month in most cases. A noticeable effect was also noted in the depletion of the numbers of over-wintering individuals, especially juveniles, in comparison with other winters. A good opportunity was afforded for collecting *Stilpnochlora couloniana* Saussure and species of *Microcentrum*. On the coldest days, search was made under trees, and numerous ones were found, having been "knocked out" by the numbing cold. A large part of the *Doru lineare* (Eschscholtz) population on the reserve also suffered extinction, and I believe that such species as these, whose ranges are more generally southern than northern Florida, have their northern limits noticeably set back by such cold waves.

GEOLOGY

As a life region of the North American continent, Florida is particularly interesting because of the influences which its recent geological history of submergences and emergences from the sea have had on the nature and distribution of the biota. While no attempt is made in the present study to show the derivation of the orthopteran fauna of Florida, a number of important factors influencing the ecology and distribution of this group are understandable only in the light of the geological background.

The doming of the basement rocks in the north-central part of the state, which brought the limestone sediments closer to the surface, has produced a topography in this region quite different from that to the east in the Welaka region where the land has been

longer subjected to submergences and emergences. This difference in topography, as well as the differences in soil, are reflected in the different types of vegetation found in the two regions. In the Welaka area, as in other parts of Florida, the pattern of the habitat distribution, i.e., swamp, flatwoods, sand scrub and sandy uplands, is largely a reflection of the former shore and terrace topography produced by the Pleistocene submergences. The topography and the distribution of the various sized sand grains which occur on the reserve are probably due to the peculiarities in the washing of the Pamlico Sea over this area when it was a marine mantle. In considering the distribution of orthopteran species in Florida, one is impressed by the absence of certain ones from the Welaka area, such as *Macneillia obscura* (Scudder), *Melanoplus puer puer* (Scudder) and *Doru aculeatum davisi* Rehn and Hebard, even in habitats which are the counterparts of those which they occupy west of the St. Johns River. This probably can be explained by the isolation of the section east of the river since the latest submergence. Also, the occurrence of endemic species in this same area, notably *Melanoplus adelogyrus* Hubbell, *Aptenopedes aptera saturiba* Hebard and the undescribed race of *Melanoplus furcatus*, previously mentioned, are other evidences for the effects of these geological factors. It does not seem out of place, then, to briefly review these events of the past which have left their mark not only upon the "landscape" but upon the biota as well.

The broad and relatively flat Floridian Plateau juts southward from the continent some 500 miles and separates the waters of the Gulf of Mexico from those of the Atlantic. The eastern portion of this plateau is of sufficient elevation to project out of the sea, forming the present state of Florida. The metamorphic basement rocks of the plateau are buried to a depth of approximately 4000 feet by the sediments, most of which are limestone, which were deposited during the periods when the plateau was submerged.

The Floridian Plateau has been singularly free from catastrophic movements and has been subjected only to the slight doming of the rocks in the north-central portion. During the long history of the plateau it has been content merely with allowing the waters of the sea to wash over its surface from time to time to a greater or lesser degree.

Running southeastwardly down the central portion of the peninsular part of Florida from the northern boundary of the state to Glades County is a ridge which varies in elevation from approximately 100 to 325 feet above sea level. Surrounding the Central Highlands (Cooke 1939), except at the extreme northwestern end, are the Coastal Lowlands which vary in elevation from near sea level to 100 feet. These lowlands represent terraces (Wicomico, Penholoway, Talbot, and Pamlico) which were formed during four periods when the sea covered this part of the land during Pleistocene time.

The Welaka area was covered with water to a depth of from 75 to 90 feet during the time when the Wicomico sea stood over the Coastal Lowlands. During the periods of the Penholoway and Talbot seas, which followed the Wicomico without interruption, the depth of the sea over the Welaka area was successively shallower, approximately 45-70 feet during Penholoway and 17-30 feet during Talbot. The period of the Talbot sea was followed by a great glacial epoch during which time a large amount of water was extracted from the sea in the formation of the great ice sheets. This caused a lowering of the water to a level which has been estimated as 60 feet below the present. During this time the Welaka area was some 70-85 feet above sea level and was subjected to erosional and solutional changes. With the end of the glacial epoch, the sea returned to a level of 25 feet above the present, and again the Welaka area was flooded for the most part. The terrace which was formed during this last, the Pamlico sea, is the only one which is well represented on the reserve (Fig. 1).

SOILS

Throughout this study an attempt was made to determine the extent of correlation between the occurrence of the orthopteran species and groups of species with the soil types found on the reserve. Morse (1904) and Strohecker (1937) both found correlations of this nature, and the former based his classification of orthopteran associations largely upon the soils. Isely (1937, 1938) has presented the relation of the distribution of soil types in Texas to the occurrence of acridid species in that area, and his evidence indicates a large amount of correlation. Experience gained during the course of this investigation, as well as that gained during the summer of 1938 in a study of the scrub areas of Florida, indicates that the type of soil may be a valid criterion for the presence of some orthopteran genera and species, but not for others. The influence may be direct, through the requirement of the species for oviposition sites, but in more numerous instances the influence of the soils have an indirect effect through their influence upon the vegetation in different situations, and in such instances at least a part of the orthopteran fauna reflects the vegetational rather than the soil type. Taking the orthopteran fauna as a whole, therefore, the most satisfactory classification of habitats proved to be one based primarily on vegetation, with the soil type as one of the ultimate factors responsible for its production and in some cases entering directly into the concept of the habitat as in the Dry, Sparsely-Vegetated Sand Habitat.

Because the soils are so intimately related to the vegetational complexes which are the major orthopteran habitats, it is important to understand something of their characteristics and distribution in the Welaka area, and the extent to which they are correlated with the vegetation.

Of the eight great soil groups which are present in Florida, five of them are represented by mappable series on the reserve. They may be classified as follows (Henderson 1939):

I. Yellow Podzolic Soils.
   Norfolk fine sand; deep phase.
   Blanton fine sand; both typical and hammock phases.
II. The Dry Sands.
   St. Lucie fine sand; typical and flat phases.
III. The Ground Water Podzols.
   Leon fine sand; typical and scrub phases.
   St. Johns fine sand.
IV. The Half-Bog Soils.
   Plummer fine sand.
   Portsmouth fine sand.
V. The Bog Soils.
   Peaty Muck; marsh and swamp phases.

The locations and areal extent of the various soil series which are found on the reserve have been presented on a soils map by Laessle (1942), and such a map is not repeated here.

On the reserve, the Norfolk fine sand is characterized by having an A-1 horizon of yellowish-gray fine sand to a depth of about six inches. The A-2 horizon is pale yellow fine sand and extends to a depth of at least six feet. Nowhere in the sandhills were we able to drill to the friable sandy clay horizons with a six-foot augre. The dominant vegetation on this soil is longleaf pine and turkey oak. The relative abundance of one or the other of these trees varies considerably throughout the extent of this soil type. Even in the areas where the oaks are dominant in numbers, the pines usually dominate the oaks in height. The differences in dominance are due largely to the unequal cutting of the pines over the sandhill areas. The herbaceous stratum consists mainly of the wire grasses, *Aristida stricta* and *Sporobolis gracilis*. The gopher apple, *Geobalanus oblongifolius* is very characteristic on the Norfolk fine sand and is practically the only shrub growth found except the small turkey oak shoots which are usually thickly scattered beneath the older oak trees.

Blanton fine sand does not cover as much of the total area of the reserve as does the Norfolk fine sand, nor does it occur over any very large extent in any one place. It is scattered throughout the reserve on higher areas above the surrounding flatwoods. In many places it is closely connected with or adjacent to the Norfolk fine sandy soil.

Two phases of Blanton soil are found on the reserve, the typical and the hammock phases. The former is found only at three localities, two in the southeastern corner of the reserve north of Beecher Spring and one surrounding the area of the administration buildings and extending in a narrow belt south of the Welaka-Georgetown road at this point. Typically, this phase has a top layer of about six inches in depth which is medium-gray fine sand. Beneath this, for a depth of approximately fifteen inches, is fine sand of yellow to yellow-gray color. This, in turn, is underlain by yellow-gray splotched fine sand. The vegetation which this phase supports is dominantly longleaf pine with a subdominant growth of bluejack oak, *Quercus cinerea*. The herbaceous undergrowth is very similar to that on the Norfolk fine sand except that, on the reserve, the growth of grasses is much more dense. The hammock phase is considerably more common on the reserve. The largest area is found just west of trail 4 at the junctions of trails 6 and 7. The hammock phase is usually darker than the typical phase and may lack the splotched layer which is characteristic of the latter. The vegetation is exceedingly variable, but differs from that on the typical phase in having a dominant growth of broad-leaved evergreens, mainly large live oaks, *Quercus virginiana*. The shrub stratum is well developed, a feature which is not so pronounced on the typical phase.

Agriculturally, St. Lucie fine sand is one of the poorest soils to be found in Florida, for it consists of almost pure, white sand to a depth of from six to eight feet. It is characterized by having the upper two inches light gray in color and the remaining depth, from sixty to ninety-six inches, very white sand. This soil, if it can be called a soil at all, has probably been developed on old sand dunes, and the topography is, consequently, comparatively high and rolling.

While this soil is not favorable for most plants, a scrubby vegetation grows profusely, forming, in places, almost impenetrable clumps of scrubby dwarf oaks and other xerophytic shrubs. These rarely exceed six or eight feet in height. Among these shrubs are scattered sand pines, *Pinus clausa*, which tower conspicuously above them.

The flat phase of this soil type does not have the rolling topography of the typical phase. As a result of this, drainage is not so excessive and there is at least an indication of a hardpan at depths varying from four to five feet. The surface layer is usually somewhat darker than that of the typical phase. The vegetation approaches that found on the scrub phase of Leon fine sand, being practically indistinguishable in many cases. The sand pine is entirely lacking on the flat phase, and the wire grass, *Aristida stricta*, may be found quite commonly.

The typical phase of Leon fine sand occupies more area than any other soil between the sandhills on the east side of the reserve and the river swamps. It is found on those flatwoods areas which are slightly higher and better drained than the bordering St. Johns and Plummer soils. The Leon and St. Johns soil series are easily distinguished from the other soils in having a distinct layer of sand which is cemented together by dark brown to black organic matter which has been called a "hardpan." In the typical phase, this hardpan is rarely less than six inches in thickness and lies at depths varying from 18 inches to 36 inches below the surface. On top of the hardpan is a highly leached layer of nearly white fine sand to within six inches of the surface. The surface layer is typically of a "salt and pepper" appearance. Longleaf pine is characteristically the only common tree on this soil, but slash pine may be present in few numbers. The shrub stratum consists mainly of ericaceous plants such as gallberry, *Ilex glabra*, some *Xolisma*

fruticosa and *Cyanococcus myrsinites*. The herbaceous growth is dominated by the wire grass, *Aristida stricta*.

The scrubby phase of Leon fine sand is found on slightly elevated areas in the typical Leon flatwoods. The soil profile is little different from the typical phase except that the hardpan lies at a lower depth, from three to four feet as a rule. The vegetation found on this phase, however, differs considerably from that found on the typical. Although longleaf pine is usually found to some extent, the shrubby undergrowth of dwarf evergreen oaks simulates that found on the St. Lucie soil which was discussed above.

The St. Johns fine sand is found on slightly lower and less well-drained areas than Leon fine sand, but on higher and better drained areas than those on which Plummer fine sand is found. It is easily distinguished from the Leon series in having the top inch or two of surface soil a very dark brown or black sand and organic matter which is usually quite hard and differing from the loose salt and pepper-colored surface layer of Leon soil. Beneath this top layer the profile is very similar to that of the Leon. The hardpan layer lies at a somewhat lower depth in the St. Johns areas than it does in the Leon areas, being from two to four feet beneath the surface. On the reserve this soil supports a tree growth which is mainly pond pine, *Pinus serotina*, with a few scattered longleaf and slash pines. Over much of the flatwoods where this soil occurs, however, there are few or no trees at all. Flatwoods on St. Johns soil are very shrubby, this stratum being almost exclusively the fetterbush, *Desmothamnus lucidus*. A few saw palmettos can be found, but these are very dwarfed. *Aristida spiciformis* seems to be a diagnostic plant and *Andropogon capillipes* and *Andropogon brachystachys* are quite common, although herbaceous vegetation, in general, is very poorly developed on this soil type.

Plummer fine sand is found on the reserve on narrow belts around the ponds, on narrow belts of poorly drained and nearly permanently saturated soil adjacent to Portsmouth soil and along the narrow anastomozing fingers of low, saturated ground throughout the flatwoods. It is very wet or saturated during most of the year and is characterized by having a top layer of very dark gray sand which is approximately six inches in depth. This is underlain by lighter gray sand to a depth of three or four feet. The dominant tree growth is the slash pine, *Pinus palustris*. The undergrowth varies considerably from very shrubby or marginal thicket type to one which is grassy, with tall wire grass, sedges, and several other herbaceous plants. Saw palmettos usually grow very tall on this soil.

Portsmouth fine sand is found in an almost continuous belt adjacent to the swamps along the river. From this belt, long fingers extend into the flatwoods along water courses and very low ground. This soil differs from Plummer in having a layer of top soil about a foot in depth which is very dark gray or black because of the large amount of admixed organic matter. Beneath this the sand is light gray or nearly white for a depth of two or three feet. During much of the year this soil is under water, and, when not, is usually saturated. Along the river swamps, *Taxodium distichum*, the bald cypress, and *Nyssa biflora* are the dominant growth, with very little or no undergrowth. In the long fingers throughout the flatwoods one finds "bayhead" vegetation, consisting of the white bay, *Magnolia virginiana*, and loblolly bay, *Gordonia lasianthus*.

The bog soil or peaty muck is practically confined to a very large area along the river in the central part of the reserve and to the large swamp and marsh which covers Buzzard's Roost Point. This soil consists of an accumulation of organic matter which is mixed with some sand and silt and is usually three feet or more in depth. The state of decomposition of the organic matter varies considerably, so that the relative percentages of peat and muck are not the same from place to place. Most of the areas covered by this soil are subject to flooding by the river, and throughout the year are nearly always covered with water. This flooding has a pronounced effect upon the pH of the soil, making it more basic than would otherwise be expected. The dominant growth on the swamp phase of this soil consists of water ash, *Fraxinus pauciflora*, red maple, *Rufacer rubrum*, and the cabbage palm, *Sabal palmetto*. The marsh phase of this soil supports a dominant growth of saw grass, *Meriscus jamaicensis*, or the marsh grass, *Spartina bakeri*.

MATERIALS AND METHODS

During the summer of 1938, three months were spent in collecting Orthoptera and Dermaptera throughout the state of Florida. I thus became intimately acquainted with a considerable part of the orthopteran fauna of the state, and I learned to recognize many of the species in the field by peculiarities of flight, method of jumping, body or wing coloration, song, and other less obvious and more subtle, impressionistic qualities with which the collector gradually becomes familiar. This experience also enabled me to learn many of the plant species, vegetational associations, and soils of northern and central peninsular Florida.

This background of field work, and the subsequent study of the material collected, greatly facilitated the ecological investigation on the reserve and added to the value of its results. An important saving of time resulted, both in the recognizing of variations in plant and soil complexes and in associating particular orthopteran species assemblages with these complexes.

The field work upon which the study is based was begun during the second week in July, 1939, and was carried on during the next fifteen months until the first part of November, 1940. Residence on the reserve was continuous during this period, except for the last week in June and the first week in July of 1940. Since then, several short periods, varying from a few days to a week, were spent there during 1941 and 1942; in 1946, the three months of June, July and

August were spent on the reserve, when an attempt was made to clarify particular problems of the whole investigation. An estimated ten thousand adults and fourteen thousand juveniles were collected and preserved, and they have been placed in the Museum of Zoology, University of Michigan. These, however, represent but a mere fraction of the many thousands of individuals which were seen in the field and whose abundance, frequency, and habitat distribution were recorded.

The first one and one-half months on the reserve were spent in reconnaissance and sampling of the Orthoptera of the area; during this period a concentrated effort was made to find as many as possible of the species which I expected to occur here. Careful notes were kept on the type of situation or situations in which they were taken. Every environmental unit which presented differences of vegetation, soil, topography, water relations, etc., was examined in order that I might gain a general conception of the distribution of the species and species assemblages among these various units. At the end of this time, analysis of the data thus far obtained seemed to indicate that there were twenty-eight different types of environments scattered throughout the reserve and in which continued collecting should be carried on. Further investigation and analysis of the species assemblages later led to a recognition of but twenty-five of these as distinct orthopteran habitats, but collecting and study was carried on in the original twenty-eight different environmental situations until the end of October, 1940. No attempt was made to establish restricted or local stations within any of these different situations because, for the most part, each type of environment covers large areas or is scattered throughout the reserve in isolated patches, and it was believed that the local variations within each of the large environmental categories should be analyzed. However, certain "type localities" within each of the different environments were visited more frequently than some of the other places within them. Each environmental unit was visited as often as possible; some were studied once every two weeks, the others at more frequent intervals.

Previous to the time that the reserve came under the jurisdiction of the University of Florida, airplane photographs had been taken of the entire region along the Welaka section of the St. Johns River. A composite picture of these was made which included the entire reserve and the immediate surrounding area. Fig. 2 was drafted from this composite photograph, and the manner of dividing the reserve into squares for the purpose of locating positions in the field is shown. The airplane photograph was of extreme value in determining the exact positions and extent of the various physical and biotic features of the reserve. The preliminary survey carried on during the first one and one-half months made it possible to correlate these features with their appearance on the photograph. I was, therefore, able to trace the exact boundaries of most of the twenty-five different types of environmental situations which had been determined for study; the distribution of isolated patches of the same type of environment, as well as the spatial relationship of one environment to another, could be determined.

ORTHOPTERAN COLLECTING METHODS

A detailed account of the various methods which are used in collecting Orthoptera has been written by I. J. Cantrall (1941). Some additional notes which I found of value in collecting in Florida have been added to that paper as part of the appendix. I shall not, therefore, go over them here, for practically all of the methods there described were employed in this study. One additional note of interest, however, might be added. During the rainy season of the summer, when one can expect anything from a downpour of a few minutes to a prolonged rain of several days, and when scarcely a day passes without some rain falling, it was very difficult to set out molasses traps for any length of time without their being flooded, with the consequent loss of specimens or a dilution of the molasses to such an extent that they became ineffective. It was necessary to devise a metal "umbrella" to place over each trap. This shield was made from zinc which was cut and put together in such a way as to make a cone approximately six inches across the base. A ten inch rod was attached to the periphery of this base, and when shoved into the ground at the side of the trap the cone was suspended above the trap and water was prevented from falling into it. The top of a trap was always placed about an inch above the general level of the ground surface and the earth banked up around the projecting top, so as to prevent surface water from running in. I also came to use a heavy beating net almost exclusively instead of a lighter one such as the American net. The use of such a heavy net is imperative for collecting in the majority of the habitats found on the reserve because of the shrubby type of undergrowth, and it is the only type which can be used for collecting specimens from the gnarled and hard scrub oaks in the various habitats, especially the scrub habitat.

PLANT COLLECTIONS

The dominant plants of each vegetational unit in which repeated collecting was done were learned with the generous help of A. M. Laessle. Since he was making a survey of the vegetational associations on the reserve, and collecting the majority of the plant species within each of them, no separate herbarium was made in connection with my study. Plants were collected and brought to the laboratory only when identification of those unknown to me seemed necessary, as those upon which certain Orthoptera were feeding or those which appeared to have other significance in connection with the orthopteran species.

SOIL SAMPLES

Determination of the soil type was made in each of the vegetational associations which were studied

as orthopteran habitats. The airplane photographs were of inestimable value in connection with the making of the soil survey. The intimate relationship between many of the vegetational and soil types permitted determination of the areal extent of a soil by observing on the photograph the extent of its correlated vegetational association. These correlations were then checked by field determinations of the soil. The pH of most of the soils, as well as the degree of soil moisture, were obtained, but no other chemical or physical analyses were made.

Recording and Analysis of Field Data

All field records were kept on ruled four by six inch cards. A large number of these were carried in a metal cover which slipped into the pocket of a collecting jacket. Each collection was given a number for each habitat. These numbers ran consecutively throughout the entire period of the investigation. Thus, collecion 5 in the Mesic Hammock Habitat was given the number MH-5, etc. As many cards were used for each collection as were needed to complete the record of that collection. The data recorded included the following: data, time of day, air temperature, exact location on the reserve, phenological data, variations of the habitat from more typical situations, and a list of the species collected with their relative abundance and the stratum or microhabitat occupied and the observations on behavior.

In order to obtain the separate data included in the large number of field records and notes, it was necessary to cross-index them according to species. Since all observations on abundance, frequency, microhabitat, etc. were kept on the field cards for each species encountered in the particular habitats, the cross-index permitted easy access to information on any species in relation to all of the habitats investigated.

The information thus obtained concerning the orthopteran fauna of each environmental situation was compiled and the data placed on large graphs according to species abundances, frequencies and the microhabitats occupied. Analysis of the graphs formed the basis for the classification of the orthopteran habitats on the reserve. The final graphs which were compiled are included at the end of this paper.

THE ORTHOPTERAN HABITATS OF THE WELAKA AREA

The Basis for the Classification of Orthopteran Habitat Assemblages

In this study, the primary emphasis was not upon the determination of the specific environmental requirements and limiting factors for each species found in the Welaka area. It is hoped, however, that such physiological determinations can be made by future workers. The emphasis was placed upon the determination of the recognizable orthopteran assemblages as they occur in this area and the determination, where possible, of the general correlations which exist between these assemblages and the various types of environment. In such an approach to the subject, it may correctly be assumed that the species assemblages find, in the environments which they occupy, those factors which they require and that, to a large extent, they share similar requirements and limitations. The assemblage as a whole reflects the total or general conditions of the habitat and the species are associated because the environment comprises a variety of conditions that meet the requirements of all of them. Certain species, of course, differ from others in their minimal and optimal requirements, and these often can be determined, as in the case of specific food plants, specific oviposition sites, etc.

The various attempts by ecological students of Orthoptera to classify the species assemblages have been based upon the existence of recognizable correlations between such assemblages and the general factors of the environment; the classifications differ chiefly because of the varying emphasis placed by each worker upon the factors with which correlations were noted. In one of the earliest attempts to thus classify orthopteran habitats and species assemblages Morse (1904 and 1907), dealing with the Acrididae of eastern North America, divided them into ground-loving (Geophilous) and vegetation-inhabiting (Phytophilous) groups of species. He further subdivided these categories into Campestrian and Sylvan associations, with lesser groupings into saxicolous, arenicolous, humicolous, etc., for the geophilous group and xerophile, hygrophile, etc., in the phytophilous group. This classification has met with fairly wide acceptance and was followed by Hancock (1911). It does define certain recognizable assemblages of Orthoptera in a broad manner, and it has general validity for the Acrididae of a large area, but does not prove very helpful in understanding the orthopteran assemblages of limited areas where peculiar local conditions are often of great significance. Furthermore, it was based primarily on a single family of Orthoptera and loses much of its value when extended to the non-saltatorial families and to the Gryllidae, Gryllacrididae, and Tettigoniidae. In the assemblages of most habitats, some species live on the ground, some on the vegetation, and some in both places. *Aptenopedes sphenarioides*, for example, apparently requires of its habitat only that it be neither extremely dry nor wet, but humid, and in particular that there be an herbage stratum present. In terms of Morse's classification it is distinctly a phytophilous species. At the same time, it occurs in nearly all parts of its environment and oviposits in the soil. The entire assemblage of a habitat forms a natural ecological unit, and Morse's primary division into geophilous and phytophilous cuts across their natural groupings. His classification does not adequately take into account the species for which not a stratum nor minor habitat but the whole or major part of the environment is their living place. The emphasis is placed upon the species assemblages which show a correlation with particular situations or strata and the recurrence of such situations or strata in different types of phyto-ecological environments. It fails to convey

any adequate picture of the characteristic and recognizable species assemblages that do in fact occupy the different major environmental types. The diverse nature of the various sub-categories recognized by Morse is also confusing since they are not comparable one with another.

Most of the other ecologists who have attempted to define orthopteran habitats on the basis of the study of limited areas have based their classification primarily upon the relationships between species assemblages and recognizable vegetational associations. They have, in general, arranged the habitats thus determined in accord with the conditions of the local area studied, instead of generalizing them into broad classifications like those of Morse. A few have, in addition, attempted to explain the occurence of the different species in the habitats and the composition of the assemblages on the basis of definite environmental factors.

Vestal (1913) was among the first to analyze carefully the orthopteran assemblages of a local area (in northern Michigan) in relation to the plant associations and to take into consideration the effect of plant succession on these assemblages. His work was original and stimulating, and it has had considerable influence on subsequent ecological investigations; it is marred only by the misidentification of a number of the species with which he dealt. A somewhat similar but more detailed study of the orthopteran habitats of a region near the southern end of Lake Michigan was published by Hubbell (1922), but this lacked the dynamic viewpoint which characterized Vestal's work. The same can be said of the work of Fox (1915) on Orthoptera and orthopteran habitats in the vicinity of Lafayette, Indiana. Both of these works are purely descriptive, though they represent careful attempts to define recognizable habitat units for the group.

Several papers of a much more ambitious character have appeared in more recent years. In his work on the Orthoptera of northeastern and north-central Texas, Isely (1937, 1938) has demonstrated that there is a large degree of correlation between recognizable orthopteran assemblages on the one hand, and both soil type and plant associations on the other; he has based his classification of orthopteran habitats largely on these two factors. Strohecker (1937), working in the classic Chicago region where so much has been done on plant and animal ecology by Cowles, Vestal, Shelford, and others, studied the Orthoptera both of the dune and the forest regions. He recognized both soil and vegetational correlations and attempted further, not entirely successfully, to correlate the occurrences of the orthopteran assemblages with a few definite physical factors of the environments. Urquhart (1941), as a result of his work on the Orthoptera of Point Pelee, Ontario, has published an ecological study of the group. He has classified the orthopteran habitats primarily upon vegetational aspects, with reference also to soil, water, and topographic relations. From certain experimental work, designed to determine just what factors control occurence of the species, he concludes that the most important limiting factor is relative humidity and the resultant effect upon evaporation rate of the insect's body moisture; the soil, food plants, oviposition sites, and other factors have, in his view, little or no influence. In this respect his results would seem to be at variance with the conclusions of many other workers and in need of verification. Lastly, Cantrall (1943) completed a careful three-year investigation of the Orthoptera and orthopteran habitats of an area in southern Michigan in which the viewpoint and methods were more nearly similar to those of the present investigation than any of the others mentioned. He recognizes vegetational type, soil, and topography as of importance, but he also emphasizes the part played by minor habitats which interdigitate with the major environments.

The most practicable basis for the classification of the orthopteran assemblages of the Welaka area was found to be the principal plant associations, with the recognition of the influence of the soil, water, and topographic relations. Each of the major environments possessing distinct orthopteran assemblages was analyzed into strata, its soil and water relations were determined, and seasonal changes in the physical and biotic features were recorded. Detailed notes were kept on the occurrence of the orthopteran species found in these units, and upon the completion of the field work the distribution, frequency, and abundance of the species in relation to all of the phytoecological habitats was determined. The data, thus organized, served to emphasize the fact which has been alluded to before; the presence of the various species in a given major environment, the sandhills, for example, is owing to very different sets of factors. In general, two classes of occurrence may be recognized. In one, the species are associated with some very definite minor habitat such as a stratum or a food plant or a particular soil condition, and they occur in any major habitat which affords this particular condition. The earwig, *Prolabia pulchella*, found wherever rotting wood in a certain stage of decay is present, is an example of this class. At the other extreme are species which occur in a wide variety of situations within the major habitat, making use of different parts of it at different times of the day, as in the case of many of the roaches, or using different areas during the various developmental stages. These have their occurrence apparently determined by the entire combination of features which enter into the composition of the habitat. Many of the grasshoppers belong to this class, and *Aptenopedes sphenarioides* may be cited as a specific example. All gradations from one of these types of occurrence to the other are represented in the orthopteran fauna of the Welaka area. The two different classificational concepts, each valid and useful within limits, would require some method of two or even three-dimensional representation to give adequate expression to the facts. Since this is impracticable, some compromise treatment was required which would fit the majority of the species rather than a selected group.

In this study, the difficulty was met, as nearly as possible, by the classification in which the primary divisions were between the major types of environment which showed distinct differences in their orthopteran species assemblages; these primary divisions, or orthopteran habitats, were thereupon further divided as needed into strata and the other minor habitats which are indicated in the discussions of the various habitats.

THE QUANTITATIVE COMPOSITION OF ORTHOPTERAN ASSEMBLAGES

It is not enough that one merely determine the various species assemblages in the different habitats of an area, for this would give only a general picture of the occurrence of the groups and would disregard the quantitative composition and the relative importance of the various species within the assemblages. The analysis of orthopteran populations in relation to habitats has been a difficult problem and a matter of much discussion since the beginning of ecological studies on this insect group. Two separate concepts are involved, that of frequency and that of abundance. Cantrall (1943) has given a thorough discussion of these concepts, and they need not be further elucidated here, for I concur with him fully. It is sufficient to say that both concepts must be taken into consideration in attempting to determine the habitat preferences of each species and the composition of the habitat assemblages. Failure to recognize this distinction in concepts, or complete failure to apply frequency-abundance data to the study of the distribution of orthopteran populations has led to confusion and often an erroneous picture of the ecological relations.

A thorough knowledge of the different species, their habitat preferences, behavior, and variations in habits were used as the basis for making quantitative estimates in this study. When collecting was done in a particular habitat a certain amount of time was first spent in finding out what species were present at that time. Another interval of time, usually from two to three hours, was devoted to the gaining of an impression of the abundance of each species, based upon the number collected, observed, or heard in relation to the length of time spent in these observations. This impression of abundance was then recorded after each species according to a four-term scale, abundant, common, numerous, or few. The last term was not usually used, but the actual number of individuals was recorded. No absolute computation of numbers of individuals per unit of time could be made which would correspond to the scale of terms listed above. Abundant does not, therefore, always mean that more than one-hundred individuals could be collected in an hour's time, or that numerous is equivalent to thirty to forty individuals collected in the same interval of time. Certain species on the reserve are so thinly scattered that even when most abundant one could not collect one-hundred individuals in several hours time. The impression of abundance was, therefore, further based upon a conception of the total population of each species as it occurred on the reserve during the time this investigation was being carried on. The determination of frequency of a species in a habitat is more easily and objectively determined. Provided that a thorough investigation is made for each species in the habitat at each collecting period, then the frequency of occurrence of the species in the habitats is a simple calculation based upon the number of times a particular species is found in a habitat in relation to the number of times collecting was done in that habitat.

The chief criticism of the method for the determination of species abundance discussed above lies in its subjectivity. Abundance is represented by a mental impression rather than by actual numbers. However, the impression is not a haphazard one and involves more rationality than at first appears. Daily observation of the species and a familiarity with their activities makes the reliability of the method approach that of an exact numerical count. Isely (1937) has expressed this view by saying, "Whatever may be the methods used in enumerating acridian populations, the writer is thoroughly convinced that an intimate acquaintance of the habits of the species, a knowledge of their seasonal behavior, life histories, and local distribution are greater aids in the determination of the acridian populations than any technique of capturing or counting with which he is acquainted." Uvarov (1928) has been slightly more emphatic on this point, and he states, ". . . it is hardly possible to evolve a method that would make possible an absolutely exact valuation of relative numbers of various species in the association; I do not even think that it would be wise to adopt such a method, even if it were found, since it would tend to minimize the importance of direct observations and subjective impressions, which are of immense value in all biological work."

For purposes of description concerning the composition of orthopteran assemblages, workers have used several systems of quantitative designation. They have assigned certain categories of abundance, frequency, or both, and they have placed the species in these categories in accordance with the data which they obtained. Vestal used six definite divisions in the scale of abundance and frequency to which species could be allocated. They are as follows: "dominant" was used for those species which have a relatively high frequency and which are usually found in considerable numbers; "frequent" referred to those species occurring regularly in the habitat, though not always found and seldom numerous when found; "occasional" was applied to those occasionally found in the habitat, not frequently and not abundantly; "infrequent" was used for those specees not often found in the habitat; and "accidental" designated those occurring in a habitat unusual for the species. Most workers have adopted systems similar to that of Vestal, using more or fewer categories and some basing the categories merely on abundance. Uvarov (1928) has listed the categories used by Kosminski (1925) in his work on the ecology of the Orthoptera

of the virgin forests of Bialowieza. Since they are on a somewhat different basis, they are of interest. "Leading species" designated those which occurred only in a particular habitat; "typical" was used for those species which were more numerous in the habitat under record than in any of the others; "not typical" referred to those which were more, or equally numerous in other habitats than in the one studied; and "occasional" designated those which were not regular members of the association.

Cantrall (1943) has presented a very noteworthy contribution to the quantitative analysis of the orthopteran populations in relation to the environments in which they occur. He was able to distinguish three grades of occupancy of a habitat by a species. (1) Permanent occupancy was applied to species where the occurrence in a given habitat was with a high frequency and usually with a high abundance, although the latter quality might fluctuate from season to season. Such species find optimum conditions in the habitat in all stages of the life history, and conditions of the environment never exceed their limits of toleration. Species which showed this relation to the habitat he termed "characteristic." (2) Semipermanent, occasional or periodic occupancy described the occurrence of a species in a habitat where it might be found for one or more generations, but in which recurrent conditions of the environment intolerable to the species prevented continuous occupancy and periodic repopulation is necessary during favorable periods. Such occupancy he has called "sporadic." (3) Impermanent occupancy referred to the occurrence of scattered, wandering individuals, or at times even of rather abundant populations of species in a habitat where survival was not possible for any length of time. Species showing this relation to the habitat were termed "erratic." While this is a meritorious attempt to elucidate the relationships of the different species to one another in the habitat assemblages and the relations of the assemblages to the various environments, it is in a large measure theoretical, as Cantrall is well aware. Determining the status of the species on the basis of the above classification necessitates long study of the species of each habitat over many seasons, and controlled experiments would be necessary to definitely place a species in any one of the categories. Because of the relatively short period which I could devote to this field study, covering a little over one complete year, it was not possible to make any such analysis of the orthopteran assemblages in the Welaka area.

In treating the orthopteran assemblages of the various habitats of the Welaka area, I have used a slight modification of those systems proposed by Vestal (1913), Rogers (1942), and Cantrall (1943). The four categories adopted are the following: the term *dominant* refers to those species which occur in a habitat with both a high frequency and high abundance; *frequent* defines those species which have a rather high frequency (perhaps 75%), and which may be either few or numerous; *occassional* was used for those which have a still lower frequency (ranging from 25% to approximately 50%) and a variable abundance which may, on occasion, be high, but is not usually so; and *infrequent*, to which belong those species which have a very low frequency of occurrence and which are usually found in small numbers in the habitat, although they may be numerous to common or even abundant in particular situations.

On the basis of frequency and abundance, many more categories might evidently be made. However, it would be impracticable and even misleading from several standpoints to attempt a classification that would recognize fine gradations in these factors. In the first place, the data on abundance are based on field estimates which are admittedly and justifiably inexact, and no statistical magic or categorical system can make the final estimates more exact and reliable than the original ones. The estimate of frequency is somewhat better adapted to numerical representation, being the ratio of the number of times a species was found to the number of times collecting was done in the habitat, but even here numerous factors of error are involved. Secondly, even were the original data sufficiently accurate to warrant the adoption of a finely discriminating scheme, each of the categories would be less easily defined, with vague boundaries between them, and it would also tend to obscure, through overemphasis on detail, the broad picture of the orthopteran habitat relations which has been attempted. Lastly, subsequent investigation is unlikely to shift any considerable number of species from one of these broader categories to another, while even one more season's work on the reserve would be certain to alter the exact status of a large proportion of them were they more narrowly limited.

In the descriptions of the orthopteran habitats which follow this section, the species assemblages in the different environments are first divided into the dominant, occasional, frequent, and infrequent species, as already discussed above. The frequency and abundance data for each species then are generalized in the following manner: the number 1 refers to low frequency, averaging 25% or less of the maximum frequency attained by the species; the number 2 describes a moderate frequency, averaging about 50%; number 3 equals relatively high frequency, averaging approximately 75%; and number 4 is used for the maximum frequency attained by the species, approaching 100%. Similarly, range of abundance has been indicated by four letter symbols. The letter A (abundant) equals the maximum number of individuals attained by a species in a habitat on the reserve; the letter C (common) refers to an abundance somewhat less than A, averaging perhaps 75% of the maximum; the letter N (numerous) is used where the number of individuals is moderate, averaging 50% of the maximum; and the letter F (few) designates numbers averaging 25% or less of the maximum.

The strata and other minor habitats of the major environment are also indicated in the descriptions of the various habitats. The stratum (for which the

symbol (s) is used) in which each species is commonly found is given.

DESCRIPTIONS OF THE ORTHOPTERAN HABITATS

XERIC ASSOCIATIONS

The xeric habitats fall into three groups on the basis of their vegetational composition; those which are sparsely vegetated or of an herbaceous type, those which are dominated by trees and shrubs, but which are not of a hammock type, and the dry type of hammock.[1] All of these habitats, because of the drainage or influences imposed by man, are decidedly more xeric than the other habitats found on the reserve.

From the standpoint of the plant ecologist, the sparsely vegetated and herbaceous group of habitats are unnatural ones which would not normally be expected in an area which had been unmolested by human agencies. In them, conditions have been forced back to the initial stages of the psammoseres. They comprise three orthopteran habitats which have been designated the Dry, Sparsely-Vegetated Sand Habitat, the Lawn Habitat, and the Dry, Ruderal Grassland Habitat. The Dry, Sparsely-Vegetated Sand Habitat occurs on the three major types of sandy soil which are the active dune or strongly wave-washed sands, residual sands, and the washed and sorted marine sands. The Dry, Ruderal Grassland Habitat may occur as a successional stage between the bare sands and the longleaf pine flatwoods or longleaf pine-turkey oak vegetational associations. Cutting and clearing in the xeric and mesic hammock causes a reversion to a grassy type of growth which is here also included in this habitat. The Lawn Habitat is a complex of plant growths and has been produced by modifications of the original conditions by landscaping, cutting of timber, and even by the covering over of the original soil with clay in a number of places. For these reasons, it 's difficult, if not impossible, to fit this habitat into any scheme of vegetational succession.

The xeric non-hammock and the xeric hammock habitats are natural vegetational complexes which are found characteristically throughout the Peninsular Lake Region, with slight modifications from place to place. The xeric non-hammock group, from the vegetational point of view, is made up of three separate complexes representing three more or less parallel developmental stages of psammoseres. The sand pine and dwarf oak, along with the longleaf pine and turkey oak vegetational associations, are comparable fire climaxes which have reached this development by parallel succession from active dunes and strongly wave-washed sands on the one hand and from residual sands on the other. The longleaf pine-saw palmetto and wire grass vegetational association is another fire climax stage comparable with the other two, but has developed on marine sand which has been washed and sorted. The higher portions of the latter have shown a succession toward the scrubby type of plant growth which is very much like that of the sand pine and dwarf oak association.

When the orthopteran fauna is taken into consideration in relation to these vegetational complexes, it is found that they form two habitats rather than three. I have called these the Scrub Habitat and the Sandhills Habitat. The orthopteran Scrub Habitat embraces the sand pine-dwarf oak-saw palmetto scrub and scrubby flatwoods vegetational associations, while the Sandhills Habitat coincides with the longleaf pine-turkey oak vegetational association.

The hammock group of the xeric associations includes only one orthopteran habitat, the Xeric Hammock Habitat. This corresponds to the xeric hammock vegetational association. It should be pointed out that this vegetational association is a successional stage through which all of the above-named non-hammock associations pass.

DRY, SPARSELY-VEGETATED SAND HABITAT

A rather large area of open sand (Fig. 3), almost completely devoid of vegetation, occurs southeast of the artificial fish ponds at the north end of the reserve, located in sections G-33, 43 on Fig. 2. Bare sand is to be found only at the eastern end of this section, the western part supporting a heavy growth of herbage. Collecting in this type of situation was most commonly done on this area since it was most representative of the habitat.

FIG. 3. Dry, Sparsely-Vegetated Sand Habitat. Area of almost bare sand southeast of the north fish ponds. March 21, 1941.

Other areas of the habitat occur as sand roads through the Scrub Habitat. Since, on the reserve, the tree stratum of the scrub is not well-developed and the shrub stratum is relatively low, the roads through these areas are subjected to almost as intense sunlight as the main area of the habitat mentioned above, and the poor, loose, sandy soil prevents an herbaceous growth. The roads through the Sandhills Habitat are also free, for the most part, from an herbaceous growth, but since the tree stratum is

[1] I have followed Laessle (1942, p. 35) in restricting the term hammock, at least as applied in Florida, to those hardwood forest associations dominated by broad-leaved evergreen trees, as distinguished from those which are merely hardwood forests. The deciduous hardwood forests are not included in the term hammock.

well-developed, these roads are shaded, and species like *Trimerotropis citrina* Scudder and *Dissosteira carolina* (L.) are absent. Most roads through the other habitats support a growth of low herbs and some shrubs, except in the actual wheel tracks. Many of these roads on the reserve have been surfaced with a reddish, sandy-clay, and, in general, these support few, if any, plants. The clay-surfaced roads are situated mainly around the boundary line of the reserve and have wide fire lanes on either side so that they receive direct sunlight for all or most of the day. They have been included as part of the Dry, Sparsely-Vegetated Sand Habitat.

In addition to the above-named areas, there are a number of smaller dry sandy spots scattered throughout the reserve which are practically devoid of vegetation and are included in the present habitat. It will be noted that, as a whole, the habitat includes a number of types of situations differing in physical conditions and in the type of adjacent habitats, both of which factors influence the orthopteran assemblage present. It is difficult, therefore, to show the limits of the assemblage associated with this environment. I have included those species which, in my judgment, are most generally found on all types of bare soil throughout the Welaka area.

The orthopteran assemblage found in this habitat comprises a total of twelve species.[2] Two strata are present, (1) the hypogeic, and (2) the terrestrial. Eight of the twelve species are members of the bare ground-loving Oedipodinae, and three of these are highly characteristic, along with *Scapteriscus acletus* R. & H. which is found in the hypogeic stratum.

Dominant: *Chortophaga australior* R. & H. 4-A, s2; *Scirtetica marmorata picta* (Scudder) 4-C, s2; *Psinidia f. fenestralis* (Serville) 4-A, s2; *Scapteriscus acletus* R. & H. 4-A, *s1* s2.

Frequent: None

Occasional: *Orphulella p. pelidna* (Burm.) 2-A, s2.

Infrequent: *Arphia granulata* Saussure 1-N, s2; *Pardalophora phoenicoptera* (Burm.) 1-N, s2; *Dissosteira carolina* (L.) 1-A, s2; *Spharagemon c. collare* (Scudder) 1-A, s2; *Trimerotropis citrina* Scudder 1-A, s2; *Melanoplus femur-rubrum propinquus* Scudder 1-F, s2; *Gryllulus assimilis* (Fab.) 1-F, s2.

Although *Scapteriscus acletus* requires a certain amount of moisture in the soil, and is also characteristic of the Moist, Sparsely-Vegetated Sand Habitat, it is able to live in rather dry situations if the subsoil is moist. During the driest weather the burrows of this species extend downward from a foot to a foot and one-half below the ground level and individuals appear at the surface only at night when the humidity is high. This species is not found on the roads through the Scrub Habitat.

LAWN HABITAT

This habitat was studied almost exclusively as it occurs about the administration building and laboratory, the dormitory building, mess hall, and garages. These buildings are all located together in the sections G-53, 54, 55, 63, 64, 73, 74, 75 on Fig. 2. Here, a large amount of landscaping has been done with shrubs, date-palms, small live oaks and other plants having been set out. The lawn, as a habitat, presents a variable composite of conditions which are extremely artificial.

Much of the terrestrial stratum of this habitat might well be considered as a part of the Dry, Sparsely-Vegetated Sand Habitat, for the soil is completely bare over rather large patches. Bermudagrass, *Cynodon dactylon* (L.) Pers., was planted on all of the lawns, but it has not succeeded very well in becoming established. The lawns are continually mowed during the spring, summer, and fall months, so that many species of plants which would ordinarily be present in such a situation are absent. Aside from the grasses, most of the herbaceous growth consists of small, thinly spaced weeds, among the most common of which are *Oxalis stricta* L., *Crotalaria rotundifolia* (Walt.) Poir., *Mollugo verticillata* L., *Krigia virginica* (L.) Willd., *Rumex hastatulus* Baldw., *Linaria canadensis* (L.) Dumont, *Cenchrus echinatus* L., *Cenchrus pauciflorus* Benth., *Paspalum ciliatifolium* Michx., *Cyperus retrorsus* Chapm., *Cyperus globulosus* Aubl., *Richardia scabra* St. Hil., *Digitaria sanguinalis* (L.), and numerous others.

The shrub and small tree stratum consists almost entirely of planted species, set out in rows along walks, driveways, and at the sides of buildings, and it is, therefore, not a continuous stratum. The shrubs are largely *Abelia grandiflora* Rehd. and clumps of the ornamental, shrub-like bottle brush, *Callistemon lanceolatus* D. C. Dense growths of bamboo have been planted in several places, mainly around the garages, and small date palms have been placed near the administration buildings and the dormitory. Numerous small live oaks, about ten feet high, are planted between the administration building and the dormitory, and these may be included in the small tree stratum along with the date palms.

The tall tree stratum is very poorly developed and discontinuous. It consists of a few longleaf pines which were left standing when the land was cleared to erect the buildings, and rows of large cabbage palms, *Sabal palmetto*, planted along the driveways and along the Welaka-Georgetown road.

An athletic field was constructed on a large open area northeast of the garages and tool house. Many truck loads of yellow sandy clay were spread over the sandy soil, rolled, and seeded with grass. The grass and small weeds developed more profusely here than on the other parts of the lawn, and this portion of the Lawn Habitat is of interest because of the large population of *Nemobius fasciatus socius* Scudder which became established. This species is very abundant here and is restricted to the area on which the clay had been spread. Its ability to survive seems to be correlated with the greater water-holding power of the clay soil and the rather heavy growth of grass

[2] The frequency and abundance for each species within the habitat as a whole is indicated by a numeral and a letter as discussed on page 93. The stratum or strata which the species occupies also is given. The most typical stratum or strata is/are *italicized* where more than one stratum is shown.

which prevented evaporation, thus producing a moist environment necessary for the species.

Fifteen species were found to constitute the orthopteran assemblage of this habitat. These forms are distributed among five strata which are (1) the hypogeic stratum, (2) the terrestrial stratum, consisting of the bare soil and the relatively bare ground beneath the vegetation, (3) the herbaceous stratum, (4) the shrub and small tree stratum, and (5) the coniferous arboreal stratum.

Dominant: *Orphulella p. pelidna* (Burm.) 4-C, s2; *Orchelimum minor* Bruner 4-C, s5; *Conocephalus f. fasciatus* (DeGeer) 4-C, s3; *Miogryllus verticalis* (Serville) 4-A, *s2* s3; *Nemobius fasciatus socius* Scudder 4-A, *2s* a3; *Scapteriscus acletus* R. & H. 4,A, *s1* s2.

Frequent: *Odontoxiphidium apterum* Morse 3-F, s2 *s3; Gryllulus assimilis* (Fabricius) 3-C, s2.

Occasional: *Scapteriscus vicinus* Scudder 2-A, *s1* s2.

Infrequent: *Labidura riparia* (Pallas) 1-A, s1 s2; *Gonatista grisea* (Fabricius) 1-A, s4; *Montezumina modesta* (Brunner) 1-N, s4 s5; *Amblycorypha uhleri* Stal 1-F, s4; *Microcentrum rhombifolium* (Saussure) ?-F, s5; *Belocephalus s. subapterus* Scudder 1-N, s4.

In addition to *Nemobius fasciatus socius*, *Scapteriscus acletus* and *Scapteriscus vicinus* were plentiful on the athletic field which had been covered with clay, as already explained. Most of their burrows extended down into the sandy soil beneath the clay, however, or at least to the junction of the sand and clay. Several specimens of *Gonatista grisea* were found on the bark of the small live oaks in the yard.

DRY, RUDERAL GRASSLAND HABITAT

The term "ruderal," as used in this paper, applies to those situations in which the vegetational complex has been considerably altered through the activities of man (except for fire and lumbering) and, as a result, the vegetation growing in these situations is not that which would be developed under undisturbed natural conditions.

A number of ruderal grassland environments have been grouped together under this habitat heading. While each variant might have been designated as a separate habitat, this would have introduced endless complexities and would have obscured the general features common to all phases of the environment. The situations which form this habitat are designated below.

Old Fields: Two fields, once cultivated, but abandoned for a number of years, were studied. One occurs just east of the site of the house which stood at Johns Landing and the other is located in the northern part of the reserve in section G-11. In these fields the vegetation consists mostly of herbaceous perennials, dominant among which are *Eupatorium compositifolium* Walt., *Andropogon virginicus* L., *Andropogon elliotii* Chapm., *Eragrostis* supp., *Pityopsis graminifolia* (Michx.) Mitt., *Cyperus retrorsus* Chapm., *Cyperus pollardi* Britton, *Paspalum ciliatifolium* Michx., *Paspalum pubescens* Muhl., *Panicum arenicoloides* Ashe, and *Panicum ovale* Ell. Another rather large field occurs just south of the fire tower, but this has been plowed annually and the vegetation consists mostly of low annuals. This field was not studied, and it has not been considered in the discussion of the habitat.

Areas cleared and plowed, but not cultivated: The airplane field, the old quail hatchery enclosure, and the area located in sections G-42, 43, 52, 53 were cleared and plowed but were never under cultivation. Only the western end of the latter area is included as a part of this habitat, the eastern end being entirely devoid of vegetation and included in the Dry, Sparsely-Vegetated Sand Habitat. These areas lack many of the weeds found in the abandoned fields and, because of incomplete plowing and grubbing, many of the plant species present before the land was cleared have become reestablished, especially some of the shrubs. Prominent grasses and other herbs are *Eragrostis* spp., *Digitaria sanguinalis*, *Andropogon* spp., *Panicum chamaelonche* Trin., *Panicum portoricense* Desv., *Gymnopogon* spp., *Cyperus* spp., *Rynchospora* spp., *Axonopus* spp., *Polypremum procumbens* L., *Diodella teres* (Walt.) Small, *Chamaecrista aspera* (Muhl.) Greene, *Galactia elliotii* Nutt., *Laciniaria* spp., and *Erechtites hieracifolia* (L.) Raf.

At the northern end of the airplane field a drainage ditch has been constructed along the edge of lower ground and the vegetation here is more characteristic of moist soil. This section of the airplane field has, therefore, been included in the Moist, Ruderal Grassland Habitat.

Firelanes: The firelanes on the reserve (Fig. 4) were plowed in April and October during the period covered by this study. As a consequence of this repeated disturbance, the herbaceous vegetation on them is not very stable and consists mainly of annuals which set their seed between the periods of plowing. During the summer months, after the lanes are plowed in the spring, the most common herbs in the firelanes running through the drier uplands are *Digitaria sanguinalis* (L.) Scop., *Cyperus martindalei* Britton, *Meibomia purpurea* (Mill.) Vail, *Stenophyllus barbatus* (Rottb.) Britton, *Stenophyllus ciliatifolius* (Ell.) C. Mohr, *Chamaecrista aspera* (Muhl.) Greene, *Chamaecrista procumbens* (L.) Greene, *Cyperus microdontus* Torr., *Isopappus divaricatus* (Nutt.) T. & G., *Glotidium vesicarium* (Jacq.) Harper, *Setaria lutescens* (Weigel.) F. T. Hubb., and *Heterotheca subaxillaris* (Lam.) Britton & Rose. Plants which spring up after the fall plowing are mostly winter annuals, the common species being *Gnaphalium spathulatum* Lam., *Gnaphalium purpureum* L., *Gnaphalium falcatum* Lam., *Sophia pinnata* (Walt.) Britton, *Lepidium virginicum* L., *Linaria canadensis* (L.) Dumont, *Linaria floridana* Chapm., *Erechtites hieracifolia* (L.) Raf., *Lactuca graminifolia* Michx., *Vicia acutifolia* Ell., *Silene noctiflora* L., *Rumex hastatulus* Baldw., *Ptilimnium capillacium* (Michx.) Raf., *Sphenopholis obtusata* (Michx.) Scribn., and

FIG. 4. Firelane south from trail 8 to the Norwalk Ferry landing. That portion of the firelane in the foreground is a part of the Dry, Ruderal Grassland Habitat. The dominant grass is *Andropogon virginicus*. The portion of the firelane through the low hammock in the background is a part of the Moist, Ruderal Grassland Habitat.

numerous other less common species. The perennials which survive in the firelanes because of their ability to reproduce asexually are *Andropogon virginicus* L., *Cynodon dactylon* (L.) Pers., *Cyperus rotundus* L., *Panicum hemitomon* Schult., and *Stachys floridana* Shuttlw.

Roads and road-shoulders: The roads present on the reserve may be classified as paved roads, shell roads, clay roads, and sand roads. The paved Welaka-Georgetown road has no vegetation growing on it, unlike most of the others on the reserve, but along the shoulders is a luxuriant weed growth composed of many species and very similar to that found in the old fields. Since these shoulders are mowed at least once a year, more annuals are found than in the fields.

The shell roads have a characteristic flora which seems to be definitely correlated with the basic nature of the road material or some mineral which is provided. The flora is similar to or identical with that found in the excavations on the shell mounds, probably in part because the seeds were carried along with the shell when the roads were constructed. The common plants are *Abutilon pauciflorum* St. Hil., *Stenotaphrum secundum* (Walt.) Kuntze, *Modiola caroliniana* (L.) G. Don., *Vicia floridana* S. Wats., *Acalypha ostryaefolia* Riddell. and *Triodia flava* (L.). This herbaceous growth is usually mowed once a year, as is the vegetation on the other roads throughout the reserve.

The clay roads, as previously stated, do not have much vegetation growing on them. *Panicum adspersum* Trin. seems to be the only plant which has become established either on the clay roads or along their margins. These roads have been included with the Dry, Sparsely-Vegetated Sand Habitat.

The sand roads which have been graded are generally well-drained, and the vegetation they support is similar to that of the fields. The continual passage of automobiles over these roads, along with the mowing, tends to keep down the taller weeds, and, consequently, the flora consists mainly of low-growing species such as *Axonopus compressus* (Swartz.) Beauv., *Digitaria sanguinalis*, several species of *Panicum*, *Paspalum*, and *Eragrostis*.

The wide variety of conditions included under the heading of Dry, Ruderal Grassland makes it difficult to define the orthopteran assemblage of the habitat as a whole. To draw a completely accurate picture of the assemblage would be to analyze in detail each of the environmental complexes which form the habitat. In addition to the variable nature of the vegetation of the various ruderal situations described, other complicating factors enter into the development of the species assemblages associated with these various conditions. Thus, in the case of the firelanes, roads, and roadsides, where mowing or plowing markedly and repeatedly disturb the herbaceous vegetation, the species assemblages are extremely variable from place to place. Plowing kills most of the eggs of those species which deposit them in the ground, and only those eggs survive which are laid in suitable areas adjacent to the plowed ground. The disturbed areas must be repopulated from undisturbed tracts. It must also be noted that when the firelanes are plowed and the roads mowed, they revert more or less toward the environmental conditions found in the Dry, Sparsely-Vegetated Sand Habitat and such species as *Chortophaga australior*, *Scirtetica marmorata picta*, *Orphulella p. pelidna* and *Pardalophora phoenicoptera* are found in these places. As the vegetation redevelops, most of these species either succumb or seek more suitable living places nearby. The species assemblages also show considerable variation because of the incursion of individuals into them from adjacent areas. While this is true in all of the habitats, it is more evident in the ruderal grassland habitats because of the larger number of species which, during at least a part of their existence, find an open, herbaceous type of growth suitable.

It has been necessary, in the light of the difficulties and complexities discussed, to generalize considerably in the analysis of the orthopteran assemblage associated with the Dry, Ruderal Grassland Habitat as a whole. Three strata are recognizable in this habitat according to the distribution of the species. These are (1) the hypogeic stratum, (2) the terrestrial stratum, which may be divided into two ecological niches

or micro-habitats (2a) the relatively open, bare soil and the bare soil beneath vegetation and (2b) the duff and debris on the ground beneath the vegetation, and (3) the herbaceous and scanty shrub stratum.

Dominant: *Radinotatum c. carinatum* (F. Walker) 4-A, s2a *s3; Mermiria picta* (F. Walker) 3-C, s3; *Schistocerca alutacea* form *rubiginosa* Scudder 3-C, s3; *Schistocerca a. americana* (Drury) 3-A, s3; *Scudderia texensis* Saussure & Pictet 4-A, s3; *Belocephalus s. subapterus* Scudder 3-A, s2a *s3; Neoconocephalus retusus* (Scudder) 3-A, s3; *Neoconocephalus triops* (L.) 3-A, s3; *Conocephalus f. fasciatus* (DeGeer) 4-A, s3; *Odontoxiphidium apterum* Morse 4-C, *s2a* s3; *Gryllulus assimilis* (Fabricius) 4-A, *s2a* s3; *Miogryllus verticalis* 3-A, *s2a* s3; *Nemobius ambitiosus* Scudder 4-C, *s2a s2b* s3; *Oecanthus nigricornis quadripunctatus* Beutenmuller 4-A, s3.

Frequent: *Melanoplus femur-rubrum propinquus* Scudder 3-X, s3.

Occasional: *Cariblatta lutea minima* Hebard 2-X, s2b; *Thesprotia graminis* (Scudder) 2-C, s2a *s3; Neotettix femoratus* (Scudder) 2-A, *s2a* s2b; *Paratettix c. cucullatus* (Burm.) 2-C, *s2a* s2b; *Amblytropidia occidentalis* (Saussure) 2-C, s3; *Arphia granulata* Saussure 2-A, s2a *s3; Chortophaga australior* R. & H. 2-C, *s2a* s3; *Scirtetica marmorata picta* (Scudder) 2-X, s2a; *Psinidia f. fenestralis* (Serville) 2-X, s2a; *Schistocerca damnifica calidior* R. & H. 2-X, s3; *Melanoplus k. keeleri* (Thomas) 2-X, s2a *s3; Scudderia f. furcata* Brunner 2-C, s3; *Anurogryllus muticus* (DeGeer) 2-A, *s1* s3; *Falcicula hebardi* Rehn 2-A, s3; *Hapithus brevipennis* Saussure 2-X, s3.

Infrequent: *Doru lineare* (Eschscholtz) 1-A, s3; *Cariblatta lutea lutea* (Saussure & Zehntner) 1-F, s2b; *Ischnoptera deropeltiformis* (Brunner) 1-X, s2a *s2b* s3; *Nomotettix cristatus floridanus* Hancock 1-F, *s2a* s2b; *Paratettix rugosus* (Scudder) 1-X, *s2a* s2b; *Mermeria intertexta* Scudder 1-F, s3; *Syrbula admirabilis* (Uhler) 1-X, s3; *Dichromorpha viridis* (Scudder) 1-F, s2a *s3; Romalea microptera* (Beauvois) 1-X, *s2a s2b* s3; *Gymnoscirtetes pusillus* Scudder 1-X, s3; *Melanoplus adelogyrus* Hubbell 1-X, s2a s3; *Paroxya a. atlantica* Scudder 1-F, s3; *Aptenopedes sphenarioides appalachee* R. & H. 1-F, s3; *Neoconocephalus caudellianus* (Davis) 1-X, s3; *Conocephalus gracillimus* (Morse) 1-F, s3.

Scrub Habitat

The terms "scrub" or "sand scrub" have been used by phytoecologists, as well as by the local people, to indicate a particular type of vegetation growing on almost pure sand, usually of the St. Lucie or Lakwood series. It is typified by having a dominant growth of sand pine, *Pinus clausa* (Engelm.) Vasey, which appears to be diagnostic, and evergreen shrubs. Many scrub areas are also characterized by the presence of rosemary, *Ceratiola ericoides* Michx., which is found on the higher portions of this habitat, sometimes in almost pure stands. The typical form of scrub is exemplified by large areas in Marion County.

The scrub, which is decidedly xeromorphic, is primarily composed of two vegetational strata. The upper tree stratum consists of scattered sand pines. Beneath these is a more conspicuous and more continuous stratum of dwarf oaks and other shrubs which reach a height of from four to eight feet. *Quercus chapmanii* Sarg. and *Quercus myrtifolia* Willd. form the largest percentage of the scrub oak growth, with *Quercus virginiana*, var. *geminata* next in abundance. *Xolisma ferruginea* (Walt.) Heller, the staggerbush, is slightly less abundant than the oaks, and most of these bushes are as high as the oaks. Twining over some of the vegetation are vines of *Smilax auricularia* Walt. and *Galactia elliottii* Nutt. Somewhat smaller than the oaks and staggerbush are clumps of saw palmetto, *Serenoa repens* (Bartr.) Small, which form the bulk of this undergrowth stratum in places. Somewhat smaller shrubs are found also throughout the scrub, and these consist largely of *Cyanococcus myrsinites* (Lam.) Small, *Garberia fruticosa* (Nutt.) Small and some *Desmothamnus lucidus* (Lam.) Small. The scrub palmetto, *Sabal Etonia* Swingle, *Tamala humilis* (Nash.) Small, *Ilex cumulicola* Small, *Ilex ambigua* (Michx.) Chapm. and *Amarolea americana* (L.) Small are also characteristic shrubs but are not usually found as frequently as those named above.

An herbaceous stratum is practically non-existent, except for small patches which are lower and where some organic matter seems to have accumulated. In such places, *Rynchospora dodecandra* Baldw. and *Panicum patentifolium* Nash are characteristic.

The porous nature of the soil of this habitat, coupled with the high average rainfall and temperature of the region, causes excessive leaching of the small amount of soluble mineral matter present in the almost pure sand and oxidation of the organic matter represented by dead leaves. Under the shrubs, therefore, the loose sandy soil is largely exposed, although a scant cover of leaves may be present in places. Mats of various sizes, composed of lichens, reindeer moss, and some leafy liverworts, are scattered over the bare sand.

On the reserve there are no areas on which the completely typical form of vegetation is growing. A small area of St. Lucie fine sand is found crossing trail 13 at the southeastern fence line. This small area is continuous with a larger area which runs along the west side of Beecher Spring Run outside the reserve boundaries. Among the notable differences between this scrub area and those which are more typical are the lack of *Ceratiola ericoides* Michx., *Opuntia pollardi* Britton & Rose, and some of the species of *Selaginella*.

Throughout the reserve is a type of scrub which differs somewhat from that just described. In the area studied the aggregate extent of this type was far greater than that of the St. Lucie scrub. It might be termed "semi-scrub" or scrubby flatwoods (Fig. 5). As can be seen on the diagram of the successional stages of the psammoseres (Fig. 17), this type of scrub is a stage found on higher portions of the flat-

FIG. 5. Scrub Habitat. Looking down on an area of semi-scrub showing a close view of the dense scrub vegetation. August, 1941.

woods vegetational association. An analysis of the soil horizons upon which this type of vegetation is growing indicates its affinities with the flatwoods soils, since an organic hardpan is encountered at a depth of from three to four feet. Above this hardpan the soil is well-drained, but it does not show the extreme leaching that is found in St. Lucie soil.

This type of scrub has a vegetational aspect which is very similar to that of the St. Lucie scrub, primarily because of the evergreen and dwarf, shrubby physiognomy. It differs in the absence of *Pinus clausa, Tamala humilis, Amarolea americana,* and *Ilex cumulicola.* Another notable variation is the presence of *Aristida stricta* in this type and not in the typical scrub.

The orthopteran assemblage found in this habitat comprises a total of forty species. These occupy three distinct strata or ecological niches within the major habitat. These strata are (1) the hypogeic stratum; (2) the terrestrial stratum, which may be further divided into two micro-habitats, (2a) the bare ground and ground beneath vegetation, and (2b) the leaf duff and dead wood; and (3) the shrub stratum.

Dominant: *Parcoblatta fulvescens* (Saussure & Zehntner) 4-A, *s2b* s3; *Anisomorpha buprestoides* (Stoll) 4-A, s3; *Aptenopedes aptera saturiba* R. & H. 4-A, s2a *s3; Anurogryllus muticus* (DeGeer) 3-A, *s1* s3; *Cyrtoxipha columbiana* Caudell 3-C, s3; *Hapithus brevipennis* Saussure 4-C, s3; *Orocharis saltator* Uhler 4-C, s3.

Frequent: *Cariblatta l. lutea* (Saussure & Zehntner) 3-N, *s2b* s3; *Spharagemon crepitans* (Saussure) 3-N, s2a s3; *Odontoxiphidium apterum* Morse 4-F, s2a *s3; Nemobius ambitiosus* Scudder 3-N, s2a; *Cycloptilum bidens* Hebard 3-N, *s2b* s3.

Occasional: *Radinotatum c. carinatum* (F. Walker) 2-F, s2a *s3; Schistocerca alutacea* form *rubiginosa* Scudder 2-F, s3; *Melanoplus rotundipennis* (Scudder) 2-F, s2a *s3; Melanoplus adelogyrus* Hubbell 2-N, s2a *s3; Montezumina modesta* (Brunner) 2-A, s3; *Oecanthus angustipennis* Fitch 2-A, s3.

Infrequent: *Cariblatta l. minima* Hebard 1-F, s2b; *Ischnoptera deropeltiformis* (Brunner) 1-F, s2b; *Parcoblatta virginica* (Brunner) 1-A, s3; *Stagmomantis carolina* (Johannson) 1-N, s3; *Thesprotia graminis* (Scudder) 1-C, s2a *s3; Mantoida maya* Saussure & Zehntner 1-A, s3; *Mermeria picta* (F. Walker) 1-F, s3; *Syrbula admirabilis* (Uhler) 1-F, s3; *Dissosteira carolina* (Linnaeus) 1-A, s2a; *Spharagemon collare collare* (Scudder) 1-C, s2a; *Scirtetica marmorata picta* (Scudder) 1-N, s2a; *Psinidia f. fenestralis* (Serville) 1-N, s2a; *Schistocerca damnifica calidior* R. & H. 1-N, s3; *Aptenopedes sphenarioides appalachee* Hebard 1-F, s3; *Belocephalus s. subapterus* Scudder 1-F, s3; *Atlanticus gibbosus* Scudder 1-N, s2a *s3; Ceuthophilus latibuli* Scudder 1-F, *s1* s2b; *Ceuthophilus walkeri* Hubbell 1-C, *s1* s2b; *Gryllulus assimilis* (Fabricius) 1-N, s2b; *Anaxipha pulicaria* (Burm.) 1-A, s3; *Phyllopalpus pulchellus* Uhler 1-F, s3; *Cycloptilum trigonipalpum* (R. & H.) 1-A s2b.

By far the greatest number of species are typically found in the shrub stratum which is the most conspicuous feature of this habitat. The next largest number are found on the bare sand or beneath the vegetation. Three species, *Anurogryllus muticus, Ceuthophilus latibuli,* and *Ceuthophilus walkeri* are to be found in the hypogeic stratum. They spend a large part of their existence below the ground surface but come out at night to feed and carry on other activities.

The almost complete lack of an herbaceous stratum in this habitat prevents many of the herbage-loving species from entering, and this fact is one of the essential differences between this and the other nonhammock and hammock groups of the xeric habitat association, even though the herbaceous stratum may be poorly developed in much of the Sandhills and Xeric Hammock Habitats. On the reserve, this habitat is distinct from all of the others in that *Parcoblatta virginica* and *Oecanthus angustipennis* were found to occur only in this environment. Other noticeable characteristics of the orthopteran assemblage are the presence of *Mantoida maya* which was found in greater numbers here than in any other habitat, and this species appears to be quite diagnostic of scrub areas in general throughout the state; *Aptenopedes aptera saturiba* also finds optimum conditions in the scrub and the abundance and frequency of the species is approached only by that found in

the Shrubby Longleaf-Pine Flatwoods Habitat which is closely allied to the scrub; *Anurogryllus muticus*, which occurs also in the Dry, Ruderal Grassland Habitat, was found to have a greater frequency in the Scrub Habitat, and this species appears to be semi-diagnostic of this type of environment.

Sandhills Habitat

The vegetational complex which forms this habitat has gone variously under the name of "high pine woods" (Watson, 1926), "longleaf pine-turkey oak" (Soc. of American Foresters, 1932), "turkey oak on cut over high pine" (Rogers, 1933) and "high pine" (Carr, 1940). I have followed Laessle (1942, p. 30) in naming this the Sandhills Habitat.

The largest area occupied by this type of vegetation on the reserve occurs on Norfolk fine sand along the entire eastern side north of trails 9 and 13 (Fig. 6). This is a sand ridge of gently rolling topography which stands at a considerably higher elevation than most of the other parts of the reserve. Other smaller patches on higher knobs occur throughout the reserve wherever Norfolk fine sand is present. In this environment, drainage and soil leaching are both very great and, consequently, the vegetation has a xeromorphic physiognomy.

The upper tree stratum of this habitat is formed almost entirely of longleaf pine, *Pinus australis* Michx., and turkey oak, *Quercus laevis* Walt. Throughout this area these two trees must be considered co-dominants. The pines are scattered regularly throughout the woods and are, for the most part, small second growth, ranging from 15-40 feet in height and from 4-10 inches in diameter. The pines were undoubtedly much more dominant in former years, because there are many pine stumps, some of them being a foot or more in diameter. In other parts of Florida, where virgin pine woods of this type are extant, the pines are dominant while the turkey oaks hold only a subdominant position beneath them. Fire and lumbering have a profound influence upon the character of this type of woods. The lumbering of pines, of course, allows the turkey oaks to assume a dominant or co-dominant role, whereas fires may produce an almost pure stand of pines because of their greater resistance to this agent. Other trees which may be locally common in this habitat are *Quercus cinerea* Michx., and on those areas which are somewhat lower and have more mineral and organic matter in the soil, one finds the live oak (*Quercus virginiana* Mill.). If fires are not frequent, the persimmon (*Diospyros virginiana* L.) may be present.

FIG. 6. Sandhills Habitat. Area of longleaf pine-turkey oak west of trail 10 and north of trail 11. Wire-grasses and small turkey oak shoots are a conspicuous feature of the undergrowth. The common shrub in this habitat, *Geobalanus oblongifolius*, may be seen in the extreme foreground. Photograph taken about six months after a ground fire swept through this area. August 30, 1940.

Over most of the ridge, the trees appear to be rather uniformly and quite widely spaced, permitting considerable sunlight to penetrate for all or much of the day. This openness allows an herbaceous undergrowth to develop. However, this stratum is nowhere very dense, except around the edges of the habitat. Areas of bare sand are extensive and one gets a general impression of an abundance of bare white sand forming the floor of the woods. Two species of wire-grass, *Aristida stricta* Michx. and *Sporobolus gracilis* Merr., are the dominant herbs. These grasses grow in tufts which, in places, are so close together that they form continuous patches. Such patches are evident only where the pine and turkey oak growth is low because of fire and cutting. Other characteristic herbs are *Pityopsis graminifolia* (Michx.) Nutt., *Carphephorus corymbosus* (Nutt.) T. & G., *Laciniaria tenuifolia* (Nutt.) Kuntze, *Asclepias humistrata* Walt., *Asclepias verticillata* L., *Cracca chrysophylla* (Pursh) Kuntze, *Crotalaria rotundifolia* (Walt.) Poir., *Crotalaria purshii* D. C., *Andropogon elliottii* Chapm., *Panicum ovale* Ell., *Panicum arenicoloides* Ashe, *Panicum aciculare* Desv., *Panicum malacon* Nash, *Eryngium aromaticum* Baldw., *Leptoglottis microphyllus* (Dryand) Britton, *Stylisma angustifolia* (Nash) House, *Rhynchospora grayi* Kunth, *Indigofera caroliniana* Mill. and *Actinospermum angustifolium* (Pursh) T. & G.

In most places, the shrub stratum is thinly scattered. The turkey oak shoots are dominant, and in some places they form considerable clumps. The only true shrub which is at all common is the gopher apple, *Geobalanus oblongifolius* (Michx.) Small. Others of minor importance are *Serenoa repens* (Bartr.) Small, *Ceanothus microphyllus* Michx., *Pityothamnus incanus* (Bartr.) Small, *Pityothamnus*

obovatus (Willd.) Small, *Cyanococcus myrsinites* (Lam.) Small, and *Cerothamnus pumilus* (Michx.)

Oak and pine leaves form a loose carpet over much of the floor of this type of woods. In the shallow depressions, as well as at the bottom of the deeper pockets of the forest floor, leaves accumulate in piles which may be six inches to a foot deep. Wire-grass clumps also hold the leaves in place, as do the clumps of turkey oak shoots. These leaves afford a retreat for many species of ground-loving Orthoptera.

An hypogeic stratum also is characteristic and prominent in this habitat. Both the gopher tortoise, *Gopherus polyphemus* (Daudin), and the pocket gopher, *Geomys tuza floridanus* (Audubon & Bachman), inhabit the soil, and their burrows and runways are the intermittent or permanent abodes of subterranean species of Orthoptera which will be discussed later.

On the reserve, there is another type of vegetational complex which is closely associated with the one just discussed. It occupies limited areas on the flat phase of Blanton fine sandy soil. In these areas turkey oak is lacking or found in very small numbers, its place being taken by the bluejack oak, *Quercus cinerea* Michx., which is co-dominant with the longleaf pine. The pine and oak stratum is more dense, as is also the herbaceous stratum, and the shrubs are very thinly scattered. The herbaceous growth is composed of practically the same plants that are found in the Sandhills Habitat. In areas which have been preserved from fire, the ground is completely covered with such herbs. The wire grasses are especially dense and form a thick, continuous growth throughout the whole woods. This vegetational complex was not studied very thoroughly on the reserve because of its small extent, so that whether it should be considered a separate habitat or phase of the sandhills has not been established. I have, therefore, left this type of vegetational complex out of the synopsis of orthopteran habitats, but certain species will be discussed in relation to their occurrence here.

A total of fifty-seven species were found in the Sandhills Habitat, one of the largest assemblages to be found in any of the habitats in the Welaka area. Corresponding to the vegetational stratification, the Orthoptera occur in the following strata and ecological niches: (1) the hypogeic stratum; (2) the terrestrial stratum, consisting of the micro-habitats of (2a) bare soil and ground beneath vegetation, and (2b) the accumulation of dead leaves and decaying wood; (3) the low shrub and herbaceous stratum which is divided into (3a) the herbaceous growth and (3b) the shrub growth; (4) the arboreal stratum which shows three micro-habitats, (4a) the tree trunks, (4b) the coniferous arboreal, and (4c) the broad-leaved arboreal.

The species making up the assemblage found in the Sandhills habitat show the following relationships:

Dominant: ***Prolabia pulchella*** (Serville) 3-A, s2b; *Cariblatta l. lutea* (Saussure & Zehntner) 4-C, *s2a s2b* s3; ***Parcoblatta fulvescens*** **(Saussure & Zehntner)** 4-A, *s2b* s3b; ***Thesprotia graminis*** (Scudder) 4-A, s2a *s3a s3b*; ***Radinotatum c. carinatum*** (F. Walker) 4-A, s2a *s3a*; ***Mermeria picta*** **(F. Walker)** 3-A, *s3a* s3b; *Syrbula admirabilis* **(Uhler) 4-A,** *s3a* s3b; *Amblytropidia occidentalis* **(Saussure)** 4-A, *s3a* s3b; *Arphia granulata* **Saussure 4-A,** *s2a* s3a; *Sphargemon crepitans* (Saussure) **4-A,** *s2a* **s3b**; *Scirtetica marmorata picta* (Scudder) 4-A, s2a; *Psinidia f. fenestralis* (Serville) 4-A, s2a; ***Schistocerca alutacea*** form *rubiginosa* Scudder **4-A, s3a** *s3b*; *Schistocerca a. americana* (Drury) 4-A, *s3a s3b* s4a; *Schistocerca damnifica calidior* R. & H. 4-A, s3b; ***Melanoplus rotundipennis*** (Scudder) 4-A, s2a *s3b*; ***Melanoplus k. keeleri*** (Thomas) 4-A, *s3a* s3b; *Aptenopedes sphenarioides appalachee* **Hebard** 4-A, s2a *s3a s3b*; ***Belocephalus s. subapterus*** **Scudder** 4-C, s2a *s3b*; ***Orchelimum minor*** **Bruner 3-A, s4b**; ***Odontoxiphidium apterum*** Morse 4-A, s2a **s2b** *s3a s3b*; ***Ceuthophilus latibuli*** Scudder 4-A, *s1* **s2a**; ***Nemobius ambitiosus*** Scudder 4-A, *s2a s2b* **s3a s3b**; ***Cyrtoxipha columbiana*** Caudell 4-A, *s3b* s4c; ***Hapithus brevipennis*** Saussure 4-A, s3a *s3b*; ***Orocharis saltator*** Uhler 4-A, *s3b* s4c; *Cycloptilum bidens* Hebard 4-A, s2b.

Frequent: ***Manomera brachypyga*** R. & H. 3-A, *s3b* s4c; ***Pardalophora phoenicoptera*** (Burmeister) 3-C, *s2a* s3a; ***Neoconocephalus triops*** (L.) 3-C, *s3b* s4b.

Occasional; ***Ischnoptera deropeltiformis*** (Brunner) 2-F, s2b; *Gonatista grisea* **(Fabricius) 2-A, s4b**; *Aptenopedes aptera saturiba* **Hebard** 2-C, s2a s3a *s3b*; *Scudderia f. furcata* **Brunner** 2-A, s3a; *Conocephalus saltans* (Scudder) 2-A, **s2a** *s3a*; *Atlanticus gibbosus* Scudder 2-C, *s2b* s3a *s3b*; ***Gryllulus assimilis*** (Fabricius) 3-C, s2a *s2b*; ***Oecanthus nigricornis quadripunctatus*** Beutenmuller 2-C, *s3a* s3b.

Infrequent: ***Aglaopteryx gemma*** Hebard 1-A, s3b; *Cariblatta lutea minima* **Hebard** 1-F, s2b; *Eurycotis floridana* (F. Walker) 1-F, *s2b* s4a; *Stagmomantis carolina* (Johannson) **1-N, s3a** *s3b*; *Anisomorpha buprestoides* (Stoll) **1-F, s3b**; ***Neotettix femoratus*** (Scudder) 1-F, s2a; ***Orphulella p. pelidna*** (Burmeister) 1-N, s2a *s3a*; ***Chortophaga viridifasciata australior*** R. & H. 1-F, **s2a**; ***Sparagemon c. collare*** (Scudder) 1-N, s2a; ***Romalea microptera*** (Beauvois) 1-F, s2a; *Hesperotettix* ***viridis*** *pratensis* Scudder 1-A, s3a; *Melanoplus* ***impudicus*** Scudder 1-A, s2a *s3a*; *Arethaea* ***phalangium*** **(Scudder)** 1-A, *s3a* s3b; *Montezumina modesta* **(Brunner)** 1-F, s4c; *Amblycorypha uhleri* Stal 1-A, **s3a** *s3b*; *Ceuthophilus walkeri* Hubbell 1-N, *s1* s2a; ***Miogryllus*** *verticalis* (Serville) 1-N, *s2a* s3a; ***Anaxipha pulicaria*** (Burmeister) 1-N, s3b; *Falcicula hebardi* **Rehn** 1-N, s3a.

The orthopteran assemblage of the Sandhills Habitat is very similar to that found in the Xeric Hammock Habitat. A glance at the species list of the two, and especially at the dominant species present in both, will show their close affinity. The following species, however, which were found in the Sandhills Habitat, were entirely lacking in the Xeric Hammock Habitat: ***Aglaopteryx gemma***, *Gonatista grisea*, ***Manomera brachypyga***, ***Mermeria picta***, ***Hes-***

perotettix viridis pratensis, Melanoplus rotundipennis, Melanoplus impudicus, Arethaea phalangium, Scudderia f. furcata, Amblycorypha uhleri, Conocephalus saltans, Ceuthophilus latibuli, Oecanthus nigricornis quadripunctatus, Anaxipha pulicaria, and *Falcicula hebardi*. The two habitats also differ in the frequency and abundance of the species found to occupy both of them.

Melanoplus impudicus, Arethaea phalangium, and *Conocephalus saltans* were found only in this habitat. *Melanoplus rotundipennis*, although present in small numbers in the Scrub Habitat, was almost confined to the sandhills and, on the reserve, appeared to be highly characteristic of this type of environment.

The large number of species which are able to live in this environment is, in a measure, the result of its openness and the consequent development of an herbaceous stratum, especially wire grasses, to a relatively high degree for a forest situation. Many larger openings, due to cutting and burning, also produce a more luxuriant herbaceous growth. The species list is larger than that of any other of the forest associations. The presence of a well-developed hypogeic stratum in the form of large numbers of gopher tortoise burrows, the presence of thick accumulations of leaves beneath the wire grasses, and the presence of both a coniferous and a broad-leaved arboreal stratum also help to account for this large species assemblage.

If one were to disregard the open areas where a rather luxuriant growth of herbaceous plants is present and to consider only the more closed portions of the habitat, a considerable number of the species would be dropped from the list. Such species, with the exception of *Mermeria picta* and *Syrbula admirabilis* which are highly characteristic of the more closed portions of this habitat, are found in the list of species which are dominant for the habitat as a whole.

Xeric Hammock Habitat

As was stated earlier, the xeric hammock vegetational association is a successional stage through which all of the other xeric associations pass before reaching the climax. Because of its intermediate position, all vegetational variations in the stages of development may exist. The definition of this habitat must, therefore, be a broad one which takes into consideration a broad range of characteristics. In general, this type of vegetational association may be defined and characterized by the presence of the dominant live oak, *Quercus virginiana* Mill., and a subdominant tree growth consisting of bluejack oak, *Quercus cinerea* Michx., laurel oak, *Quercus laurifolia* Michx., cabbage palm, *Sabal palmetto* (Walt.) Todd, and a few longleaf and loblolly pines, *Pinus Taeda* L.

The most extensive area of xeric hammock within the boundaries of the reserve lies, for the most part, between trails 6 and 7 just west of trail 4 (Fig. 7). These trails do not form its boundary but the bulk of the habitat is outlined by them. This xeric hammock forms a vegetational type easily distinguished from the flatwoods which entirely surround it. The dominant tree growth is *Quercus virginiana*, ranging from twenty-five to sixty feet in height. Very large oaks, however, are much fewer than those which are from thirty to forty feet high. This oak probably constitutes about ninety per cent of the taller tree growth. Scattered irregularly throughout the hammock are very large *Quercus myrtifolia*. The largest are twenty-five feet or more tall. Large *Quercus laurifolia* are to be found scattered sparingly throughout, the largest being about the same size as the average live oak. Only a few *Quercus cinerea* large enough to constitute a part of the upper tree stratum are present.

FIG. 7. Xeric Hammock Habitat. Part of the large area of live oak hammock just west of trail 4, between trails 5 and 7. Tall live oaks with long garlands of Spanish moss form the dominant tree growth. Small cabbage palms may be seen in the picture. In the foreground, the carpet of oak leaves on the ground and a few shrubs of the low shrubs stratum are shown. September, 1940.

Rather regularly spaced throughout the hammock, and in places occurring almost exclusively, are tall *Pinus australis*. A few *Pinus clausa* and *Pinus Taeda* also are present. All of the pines are at least a foot in diameter and range from forty to seventy-five feet high. Except in spots, as mentioned above, the pines are nowhere dominant.

The small tree and shrub growth consists primarily of oak shoots which vary in height from four to eight feet. These form clumps of varying sizes and densities and produce a labyrinth throughout the hammock. Small pines also are scattered throughout, about as evenly as are the taller pines. The most typical true shrubs are *Batodendron arboreum* Marsh, *Rhus copallina* L., *Callicarpa americana* L., *Polycodium floridanum* (Nutt.) Greene, and the staggerbush. Twining over the oak shoots and about the shrubs are vines of *Muscadina munsoniana* (Simpson) Small, *Parthenocissus quinquefolia* (L.) Greene, and wild bamboo, *Similax auriculata* Walt.

The hammock is rather open beneath the tree stra-

tum, but the ground is well shaded beneath the leafy canopy. Because of the shade, as well as the heavy demand upon the soil water because of the high transpiration rate, the well-drained sandy soil, and the loss of water by evaporation from the soil surface, this habitat does not have a well-developed herbaceous stratum. Where trees have been cut, however, there is a good growth of grasses and herbs. The general character of the growth in such places is a low mat of short grasses and herbs consisting primarily of several species of *Panicum*, *Lechea*, and *Pityopsis*. *Crocanthemum corymbosum* (Michx.) Britton and *Paspalum* sp. grow in smaller numbers.

Throughout those portions of the hammock where trees are more thickly spaced, the ground is covered with a layer of oak leaves and pine needles. In the openings of the tree stratum, open bare ground is conspicuous about the thinly scattered herbaceous growth. The leaf covered ground and the bare sand provide situations suitable to distinct orthopteran species which will be indicated later.

An hypogeic stratum is also evident in this habitat. Gopher tortoise burrows are everywhere throughout the hammock, and these burrows provide refuge for subterranean species during the day.

The four vegetational strata produce a stratification of the orthopteran assemblage into as many strata, with the addition of the hypogeic stratum. These may be generalized as follows: (1) the hypogeic stratum; (2) the terrestrial stratum, divisible into the micro-habitats of (2a) bare soil and ground beneath vegetation, and (2b) the accumulation of fallen leaves and decaying wood on the ground; (3) the herbaceous stratum; (4) the tall shrub stratum; and (5) the arboreal stratum which has three micro-habitats, (5a) the tree trunks, (5b) the coniferous arboreal, and (5c) the broad-leaved arboreal.

The quantitative composition of the orthopteran assemblage of this habitat and the strata which the forty-six species occupy are shown below.

Dominant: *Prolabia pulchella* (Serville) 3-A, s2b; *Parcoblatta fulvescens* (Saussure & Zehntner) 4-A, s2b s4; *Eurycotis floridana* (F. Walker) 4-A, s2b; *Pycnoscelus surinamensis* (L.) 3-A, s2b; *Radinotatum c. carinatum* (F. Walker) 3-C, s2a *s3; Amblytropidia occidentalis* (Saussure) 3-C, *s3* s4; *Arphia granulata* Saussure 4-A, *s2a* s3; *Pardalophora phoenicoptera* (Burmeister) 4-A, *s2a* s3; *Spharagemon crepitans* (Saussure) 4-A, s2a *s3; Scirtetica marmorata picta* (Scudder) 3-A, s2a; *Psinidia f. fenestralis* (Serville) 4-A, s2a; *Schistocerca alutacea* form *rubiginosa* Scudder 3-A, s3 *s4; Schistocerca damnifica calidior* R. & H. 3-C, s4; *Aptenopedes aptera saturiba* Hebard 3-A, s2a *s4; Nemobius ambitiosus* Scudder 4-A, s2a *s2b* s3; *Cyrtoxipha columbiana* Caudell 4-C, *s3* s4; *Cycloptilum bidens* Hebard 4-A, s2b.

Frequent: *Ischnoptera deropeltiformis* (Brunner) 3-F, s2b; *Neotettix femoratus* (Scudder) 3-N, s2a; *Orphulella p. pelidna* (Burmeister) 3-N, *s2a* s3; *Microcentrum retinerve* (Burmeister) 3-N, s5c; *Orchelimum minor* Bruner ?-?, s5b; *Odontoxiphidium apterum* Morse 4-N, s2a *s3 s4; Hapithus brevipennis* Saussure 3-N, s4; *Orocharis saltator* Uhler 4-N, *s4* s5c.

Occasional: *Syrbula admirabilis* (Uhler) 2-N, s3; *Romalea microptera* (Beauvois) 2-A, *s2a* s3 s4; *Schistocerca a. americana* (Drury) 2-A, *s3 s4* s5a; *Melanoplus adelogyrus* Hubbell 2-A, s2a s3 *s4; Melanoplus k. keeleri* (Thomas) 2-C, *s3* s4; *Montezumina modesta* (Brunner) 2-C, s4; *Lea floridensis* (Beutenmuller) 2-N, s5c; *Neoconocephalus triops* (L.) 2-A, s4; *Atlanticus gibbosus* Scudder 2-C, s2b *s4; Ceuthophilus walkeri* Hubbell 2-A, *s1* s2a; *Gryllulus assimilis* (Fabricius) 2-N, s2a *s2b*.

Infrequent: *Chorisoneura texensis* Saussure & Zehntner 1-A, s4; *Cariblatta l. lutea* (Saussure & Zehntner) 1-N, *s2b* s4; *Stagmomantis carolina* (Johannson) 1-N, s3 *s4; Thesprotia graminis* (Scudder) 1-N, s2a *s3 s4; Anisomorpha buprestoides* (Stoll) 1-F, s4; *Chortophaga viridifasciata australior* R. & H. 1-F, s2a; *Aptenopedes sphenarioides appalachee* Hebard 1-N, s2a *s3; Stilpnochlora couloniana* Saussure ?-A, s5c; *Microcentrum rhombifolium* (Saussure) ?-A, s5c; *Belocephalus s. subapterus* Scudder 1-N, s2a *s4; Miogryllus verticalis* (Serville) 1-F, s2b.

In the discussion of the Sandhills Habitat, the similarities between the orthopteran assemblages found there and those found in this habitat were pointed out. Species which were found in the Xeric Hammock Habitat and not in the sandhills are *Chorisoneura texensis, Pycnoscelus surinamensis, Melanoplus adelogyrus, Stilpnochlora couloniana, Microcentrum rhombifolium, Microcentrum retinerve,* and *Lea floridensis*. It is especially interesting to note the presence of *Stilpnochlora*, *Microcentrum* and *Lea* in this habitat and not in the Sandhills Habitat. There appears to be a high degree of correlation between the presence of these forms with live oaks and black oaks and they were never found to occur on the turkey oak. It is also interesting to note the complete separation of *Melanoplus adelogyrus* and *Melanoplus rotundipennis* between the Xeric Hammock and the Sandhills Habitat, the former having been found only in this habitat, whereas the latter was found only in the Sandhills Habitat. Elsewhere in Florida they have been found to occur together in various relative numbers.

The herbaceous stratum in this habitat is much less developed than in the Sandhills Habitat, except along roads and in the openings. The total list of species is, therefore, correspondingly less than in the sandhills. Such species as *Mermeria picta, Hesperotettix viridis pratensis, Arethaea phalangium, Scudderia f. furcata, Amblycorypha uhleri,* and *Conocephalus saltans* are absent largely because of this factor.

MESIC ASSOCIATION

The mesic hammock orthopteran habitat is synonymous with the mesic hammock vegetational association on the reserve. This association is considered to be the climax vegetational complex in this region

by the plant ecologists. The association has been termed "high hammock," "hammock," or "mesophytic hammock" by various authors.

Theoretically, this climax vegetational type may be attained through both the xeroseres and hydroseres. However, on the reserve, the climax hammocks appear to have been developed only through the xeroseres. As will be pointed out in the discussion of the Mesic Hammock Habitat, there is a closer resemblance between the mesic and the xeric hammocks than between the mesic and the low or hydric hammocks in regard to their orthopteran assemblages and the vegetational and physical factors. This is explainable largely on the basis of their xeroseric development, especially in this area; they are rather poorly developed and retain many of the vegetational elements of the preceding successional stages.

MESIC HAMMOCK HABITAT

On the reserve, none of the mesic hammocks have reached the typical climax stage, for all of them show remnants of earlier successional stages. No very large areas within the confines of the reserve have this climax vegetation growing on them. The best-developed mesic hammocks (Fig. 8) occur in a narrow belt between the flatwoods and the river swamps beginning just north of Mud Spring and running a little over a quarter of a mile south of this point. Mesic hammocks are found also along the river at and south of Orange Point and at John's Landing. Immediately outside of the fence bounding the southeastern part of the reserve there is another small area of mesic hammock north of Beecher Spring.

These hammocks are found on Blanton fine sand, the same soil type upon which the xeric hammock is found. However, by an accumulation of organic matter in the mesic hammocks, excessive leaching of the soil is prevented and fertility is increased. The increase in tree cover makes such a hammock less subject to wind action beneath the canopy and evaporation rates are decreased. The shading from direct sunlight tends also to increase the relative humidity within the hammock.

FIG. 8. Mesic Hammock Habitat. Mesic hammock above the boil of Mud Spring. Saw palmettos usually do not form such a conspicuous part of the undergrowth as they do in this particular place. June, 1941.

In the more moist portions of the mesic hammocks on the reserve there is a characteristic arboreal stratum composed of *Magnolia grandiflora* L., *Quercus laurifolia* Michx., *Tamala borbonia* (L.) Raf., *Hicoria glabra* (Mill.) Britton, *Ilex opaca* Ait., *Quercus nigra* L., *Padus virginiana* (L.) Mill., some *Quercus virginiana* Mill. and *Liquidambar styraciflua* L. A few cabbage palms are scattered throughout, as well as the basswood, *Tilia floridana* Small. About the margins of these hammocks loblolly pine is frequent.

The shrub and small trees stratum seems to be best developed near the margins of these hammocks and along winding courses where the ground is a little more moist than elsewhere. The stratum is, therefore, not continuous but scattered and labyrinthic. Characteristic shrubs are *Batodendron arboreum* (Marsh) Nutt., *Callicarpa americana* L., *Xolisma ferruginea* (Walt.) Heller, *Serenoa repens* (Bartr.) Small, *Amarolea americana* (L.) Small, and the small-flowered pawpaw, *Asimina parviflora* (Michx.) Dunal. Over these, forming in some places almost impenetrable tangles, grow vines of *Muscadina rotundifolia* (Michx.) Small, *Smilax bona-nox* L., *Ampelopsis arborea* (L.) Rusby, *Parthenocissus quinquefolia* (L.) Planch, *Bignonia radicans* L., and *Toxicodendron radicans* (L.) Kuntze.

Because of the heavy tree cover, allowing little penetration of sunlight, the herbaceous stratum of the hammocks is confined to clearings, roads, and other spots where sunlight does reach the ground. The herbs found in such places are practically identical with those found in the openings of the xeric hammocks. Other herbs scattered sparingly throughout the hammocks are *Panicum joorii* Vasey, *Panicum equilaterale* Scribn., *Mitchella repens* L., and *Scleria triglomerata* Michx.

The ground is covered with a fairly heavy layer of leaves and leaf mold which forms a distinct stratum for the Orthoptera. An hypogeic stratum is not well-developed here, however, for neither the gopher turtle nor the pocket gopher occur in this situation, and I have found no orthopteran species living here which construct their own burrows, and *Ceuthophilus walkeri* probably lives beneath the tree roots and perhaps in the burrows of small animals other than those mentioned.

Five recognizable strata of orthopteran occurrence are to be found in this habitat: (1) the hypogeic stratum; (2) the terrestrial stratum, composed of the two ecological niches (2a) bare soil and ground beneath the vegetation, and (2b) the leaf mold and decaying wood on the ground; (3) the herbaceous stratum; (4) the shrub stratum; and (5) the arboreal stratum, in which are found two ecological niches, (5a) the tree trunks, and (5b) the broad-leaved arboreal subhabitat.

The thirty-two species of Orthoptera found in this habitat and their relationships are as follows:

Dominant: *Cariblatta l. lutea* (S. & Z.) 3-A, *s2b* s3; *Ischnoptera deropeltiformis* (Brunner) 4-N, s2a *s2b; Pterophylla c. camellifolia* (Fabricius) 4-A, s4 *s5b; Lea floridensis* (Beutenmuller) 3-A, s4 *s5b; Atlanticus gibbosus* Scudder 4-A, s2b *s4; Nemobius ambitiosus* Scudder 4-A, s2b.

Frequent: *Eurycotis floridana* (F. Walker) 3-N, *s2b* s5a.

Occasional: *Prolabia pulchella* (Serville) 2-A, s2b; *Romalea microptera* (Beauvois) 2-A, *s2a* s4; *Aptenopedes aptera saturiba* Hebard 2-N, s4; *Stilpnochlora couloniana* Saussure ?-A, s5b; *Microncentrum rhombifolium* Saussure ?-C, s5b; *Gryllulus assimilis* (Fabricius) 2-N, s2a *s2b; Hapithus agitator quadratus* Scudder 2-A, s4; *Orocharis saltator* Uhler 2-F, s4.

Infrequent: *Cariblatta lutea minima* Hebard 1-F, s2b; *Thesprotia graminis* (Scudder) 1-F, s2a *s4; Stagmomantis carolina* (Johannson) 1-F, s4; *Anisomorpha buprestoides* (Stoll) 1-N, s4; *Spharagemon crepitans* (Saussure) 1-F, s2a; *Schistocerca obscura* (Fabricius) 1-F, s4; *Aptenopedes sphenarioides appalachee* Hebard 1-F, s3 *s4; Scudderia f. furcata* Brunner 1-F, s4; *Microcentrum retinerve* (Burmeister) ?-F, s5b; *Belocephalus s. subapterus* Scudder 1-F, s2a *s4; Camptonotus carolinensis* (Gerstaecker) 1-C, s4 *s5b; Ceuthophilus virgatipes* Rehn & Hebard 1-F, s2a *s2b; Cycloptilum bidens* Hebard 1-N, s4; *Cycloptilum trigonipalpum* (Rehn & Hebard) 1-N, s4; *Cycloptilum antillarum* (Redtenbacher) 1-A, *s2b* s4.

Although the mesic hammock is the climax stage reached through both the xeroseres and the hydroseres, as was mentioned above, there seems to be a closer affinity, at least on the reserve, between the mesic and the xeric hammocks than between the mesic and the hydric or low hammocks in regard to growth forms of the vegetation, species of plants, condition of the ground cover, soil, and in many of the other physical and biotic factors. The closer resemblance to the xeric hammocks is largely owing to the fact that the mesic hammocks on the reserve have developed through the xeroseres and not through the hydroseres, and the xeric hammock is the last vegetational association in that sere before the climax, as has been pointed out before. The similarity between the mesic and xeric hammocks is reflected by the twenty-two species which are common to both; only sixteen species are common to both the mesic and low hammock habitats.

Two of the most outstanding differences between the mesic and the xeric hammock habitats on the reserve are: the complete absence of the Oedipodinae from the former, except for a very few *Spharagemon crepitans*, which is correlated with the almost complete absence of bare soil; and the presence of *Pterophylla c. camellifolia* and *Lea floridensis* in the mesic hammocks and their absence or relative scarsity in the xeric hammock habitat. It should be noted, however, that *Lea* is found in some of the xeric areas and it has been taken also in the sandhills and the scrub.

A few of the outstanding characteristics of the orthopteran assemblage of this habitat, in comparison with the other species assemblages in the other habitats on the reserve, are the presence of *Pterophylla c. camellifolia* and *Lea floridensis* with a high frequency and abundance; the presence of *Atlanticus gibbosus* with greater frequency and abundance in this habitat than in any other; the presence of *Camptonotus carolinensis*, which was found in only one other habitat, the low hammock habitat; the high frequency and abundance of *Hapithus agitator quadratus;* the presence of *Cycloptilum antillarum* and *Ceuthophilus virgatipes* which, on the reserve, were found only in this habitat; and the presence of *Ischnoptera deropeltiformis* with a very high frequency, although this species was found in greater abundance in the low hammock habitat and in the bayhead habitat.

POORLY DRAINED OR MESO-HYDRIC ASSOCIATIONS

The habitats which here have been placed together and classified as meso-hydric occur on poorly drained soils which are moist during most of the year and may be saturated at certain times. On the other hand, some of these vegetational associations, such as the longleaf pine flatwoods and black pine flatwoods, which may be classified as meso-hydric for the greater part of the year, become quite dry during periods of little rainfall. This general classification, then, does not carry with it the idea of a stable set of conditions exactly intermediate between those in the mesic and those in the hydric associations; it implies a broad range of fluctuating conditions which lie between the two.

The meso-hydric associations may be divided into three groups on the basis of the growth form of the dominant plants; namely, those which are sparsely vegetated or of an herbaceous type, those which are dominated by shrubs, and those which are normally dominated by trees (because of lumbering or fires, some of these habitats have much fewer trees than normal, but the trees may be considered as the dominant plants in respect to growth form). The tree-dominated group has been termed "flatwoods," a name which has been long in use for these particular types of associations.

The sparsely vegetated and herbaceous group of plant associations comprise three orthopteran habitats, the Moist, Sparsely-Vegetated Sand Habitat, the Moist, Ruderal Grassland Habitat, and the Pond Margin Habitat. The first two of these develop as the result of human agencies. A number of vegetational complexes have been included within each of these habitats, and, therefore, they are not definite phytoecological units as will be pointed out in the discussion of each of them. The herbaceous Pond Margin Habitat also includes more than one type of vegetational complex, which, for the Orthoptera, may be considered as a single environment. It should be pointed out that the plant ecologist might place the

Pond Margin Habitat, as well as the Marginal Thicket Habitat, as a sub-association or vegetational type under the more inclusive slash pine flatwoods vegetational association. The former is undoubtedly a successional stage between the pond habitat and the marginal thicket habitat, while the marginal thickets appear to form a successional stage between the slash pine flatwoods and the bayhead association, and they may be a successional stage between some of the moist, ruderal grasslands and the bayheads. These relationships are shown on Fig. 17.

Large areas in Florida and adjoining parts of the Coastal Plain are characterized by flat and usually low-lying topography, with the water table not far beneath the surface. These areas of poor drainage support a characteristic type of vegetation known as flatwoods. The group of habitats within this category do not naturally fall into the xeric-mesic-hydric scheme of classification; their peculiarities are such that at times during a particular season or for a particular portion of the biota they may present hydric conditions, while at another season or for another part of the biotic assemblage they may present xeric conditions. The explanation for this unusual situation is found in the topography and relation to the water table. It is characteristic of certain flatwoods soils to develop an impervious hardpan layer at the ground-water level. During the wet season, water in the lowest portions stands an inch deep or more over the surface of the ground. It is unable to run off because of the lack of slope and unable to penetrate to the subsoil because of the hardpan. At such times the environment would be classed as more hydric. On the other hand, during periods of drought the soil above the hardpan dries out and subsoil moisture is prevented from reaching the surface layers by the presence of the same impervious hardpan. At such times the moisture conditions in these flatwoods habitats are strongly xeric. The continual repetition of such conditions, along with the acid nature of the soils, leads to the development of a vegetation containing a large xerophytic element.

Moist, Sparsely-Vegetated Sand Habitat

Two distinct edaphic conditions are included in this habitat; namely, areas of almost pure sand, very little organic matter being mixed with it, and areas in which the sand contains a large amount of organic matter and might be classified as mucky sand.

Many of the artificial fish ponds at the north end of the reserve form areas of almost pure sand. Those ponds which are drained before a heavy growth of aquatic vegetation develops and before organic matter accumulates on the bottom have almost pure sandy basins and are more moist than the other bare, sandy areas because of their lower elevation. Sometimes a growth of mat grasses and a few other low-growing herbs cover rather large patches of the bottom when they are not flooded regularly. Many of the ditches also form linear areas of this type of habitat. They are kept cleared of vegetation by repeated cleaning, and certain sections of them do not naturally support much vegetation for some reason.

Those fish ponds which are not drained for considerable lengths of time have an accumulation of organic matter on the bottom. Before an herbaceous growth develops on them they form a part of this habitat, being areas of the second type mentioned above. Areas of black, mucky sand, with very little vegetation on them are found also in the firelanes which run through St. Johns soil. Although vegetation finally becomes established on such lanes, they tend to remain free of plant growth longer than do the other lanes after they have been plowed.

Only seven species have been found to form the orthopteran assemblage in the Moist, Sparsely-Vegetated Sand Habitat. Three of the four dominant species are in (1) the hypogeic stratum. The other stratum of this habitat, (2) the terrestrial stratum, consist of two ecological niches; namely, the (2a) bare, medium wet soil, and (2b) the low, mat grass which covers large patches of the moist soil.

Dominant: *Orphulella p. pelidna* (Burmeister) 3-A, s2a *s2b; Gryllotalpa hexadactyla* Perty 3-A, *s1* s2a; *Scapteriscus acletus* Rehn & Hebard 4-A, *s1* s2a; *Tridactylus minutus* Scudder 4-A, *s1* s2a.

Frequent: none.

Occasional: *Romalea microptera* (Beauvois) 2-N, s2a *s2b; Miogryllus verticalis* (Serville) 2-N, s2a *s2b*.

Infrequent: *Gryllulus assimilis* (Fabricius) 1-F, s2a *s2b*.

Moist, Ruderal Grassland Habitat

As was the case in the Dry, Ruderal Grassland Habitat, several types of environmental conditions are included under the above heading, and each of these types might have been designated as a separate habitat for Orthoptera. Three categories of situations, however, are preëminent, and these were the ones most studied and upon which practically all of the information concerning the habitat is based. These categoriess are (1) the firelanes through low, moist or wet areas; (2) roadside or other drainage ditches; and (3) seepage areas.

Firelanes which have been formed through slash pine flatwoods generally support a very luxuriant growth of vegetation. Because of the richer, mucky soil and the suitable water relations, plants spring up quickly after the lanes are plowed and grow in great profusion. The vegetation is heaviest during the summer and early fall months before the October plowing. The growth consists largely of annuals, but since the furrows do not coincide at each plowing, some perennials survive, among the most prominent being *Andropogon* spp., *Juncus* spp., *Panicum* spp., and *Eupatorium capillifolium* (Lam.) Small.

Two firelanes on the reserve, one just south of trail 7 and running west from trail 8, and another which runs south from trail 8 along the fence line to the Norwalk Ferry landing (Fig. 4), pass into or

through low hammocks. The vegetation in these is considerably different from that in the firelanes through the slash pine flatwoods. Two chief factors account for the differences. They pass through much lower ground and have a foot or more of water over the lowest portions during the summer and fall, and in these very wet places the vegetation is much like that of the ponds, *Pontederia* and *Panicum hemitomon* Schult. being dominant. The other factor is the presence of numerous stumps and root tangles which were not grubbed out of the lanes. When they are plowed, rather wide detours are made around these stumps and roots and the vegetation on these "islands" contains more perennials and shrubs than does that of their plowed portions and of the firelanes through the slash pine flatwoods. The dominant grasses and other herbs present in these two firelanes are *Cyperus* spp., *Panicum webberianum* Nash, *Panicum verrucosum* Muhl., *Panicum sphagnicola* Nash, *Rynchospora corniculata* (Lam.) A. Gray, *Scleria* sp., *Stenophyllus* sp., *Rhexia* spp., *Cuscuta* sp., and *Eupatorium capillifolium* (Lam.) Small. Shrubs found here are *Hypericum* sp., small persimmon trees, small shoots of tupelo gum, and thick tangles of blackberry, *Rubus betulifolius* Small. The dense herbaceous growth and the presence of the dense tangles of blackberry makes the vegetation resemble that of the Marginal Thicket Habitat in general facies, if not in actual plant species. This similarity is also reflected in the presence of two species of Orthoptera which are very characteristic of the latter habitat, viz., *Melanoplus* sp. (Clypeatus Group) and *Scudderia cuneata* Morse. Other species of Orthoptera found here, however, make these firelanes more closely allied with the other areas of the Moist, Ruderal Grassland Habitat than with the Marginal Thicket Habitat.

Ditches have been dug along many of the roads on the reserve, especially along those through the flatwoods, and numerous drainage ditches are scattered throughout the reserve to provide drier conditions, where needed. These ditches do not, as a rule, have permanent water standing in them, but the soil on the bottom is usually very wet or saturated for most of the year. A large number of plant species occupy these ditches, but, in general, the flora is very similar to that around the marginal of the flatwoods ponds. The dominant herbage consists of *Andropogon glomeratus* (Walt.) B. S. P., *Dichromena colorata* (L.) A. Hitchc., *Cyperus microdontis* Torr., *Juncus* spp., some *Typha latifolia* L., *Meibomia Chapmanii* (Britton) Small, *Paspalum urvillei* Steud., *Ambrosia monophylla* (Walt.) Rydb., *Carex Longii* Mackenzie, *Ludwigia microcarpa* Michx., *Isnardia palustris* L., *Hydrocotyle umbellata* L., *Panicum hemitomon* Schult., *Panicum condensum* Nash, *Sacciolepis striata* (L.) Nash, *Eupatorium capillifolium* (Lam.) Small, *Mikania scandens* (L.) Willd., and others.

One seepage area was especially collected and studied as a part of this habitat complex. It occurs at Mud Spring, on the slope from the mesic hammock at this point down to the boathouse at the head of the spring. This slope was cleared of trees and all of the herbaceous and shrubby vegetation cut down, making the area park-like in appearance. On the south side of the path leading to the boathouse, water seeps out on the slopes and keeps the soil very wet or saturated nearly all of the year. A luxuriant vegetational growth occurs at this spot, and since it is mowed usually but once a year, becomes very dense. Prominant plants are *Panicum lucidum* Ashe, *Panicum joorii* Vasey, *Andropogon* spp., *Rhexia nashii* Small, *Callicarpa americana* L., *Galactia elliotii* Nutt., *Pluchea foetida* (L.) D. C., a few *Eupatorium capillifolium* (Lam.) Small, *Pteris latisculata* Desv., and *Osmunda cinnamomea* L.

The same difficulties are encountered in defining the orthopteran assemblage of this habitat as a whole as were evident in the case of the Dry, Ruderal Grassland Habitat, and which were there discussed. The list of species associated with the entire Moist, Ruderal Grassland Habitat complex is necessarily a generalization, and the same is true of the quantitative data.

The two strata which the species occupy in this habitat are (1) the terrestrial stratum, formed from the two micro-habitats of (1a) bare, moist soil in the open and beneath vegetation, and (1b) low mat grass which is found in some of the more moist bare areas; and (2) the herbage and shrub stratum, which may be divided into the (2a) herbaceous and (2b) shrub sub-habitats.

Dominant: *Nomotettix cristatus floridanus* Hancock 4-C, s1a; *Tettigidea lateralis lateralis* (Say) 4-A, s1a; *Radinotatum carinatum carinatum* (F. Walker) 4-C, s1a *s2a; Dichromorpha viridis* (Scudder) 4-A, s1a *s2a; Paroxya atlantica atlantica* Scudder 4-C, s2a; *Aptenopedes sphenarioides appalachee* Hebard 4-C, s2a; *Orchelimum glaberrimum* (Burmeister) 4-C, s2a; *Odontoxiphidium apterum* Morse 4-C, s1a *s2a.*

Frequent: *Oecanthus nigricornis quadripunctatus* Beutenmuller 3-N, s2a.

Occasional: *Stagmomantis carolina* (Johannson) 2-A, s2a; *Thesprotia graminis* (Scudder) 2-N, s1a *s2a; Mermeria intertexta* Scudder 2-A, s2a; *Orphulella pelidna pelidna* (Burmeister) 2-N, s1a *s1b s2a; Eotettix signatus* Scudder 2-C, s2a; *Melanoplus femur-rubrum propinquus* Scudder 2-A, s2a; *Scudderia texensis* Saussure & Pictet 2-N, s2a; *Amblycorypha floridana floridana* Rehn & Hebard 2-A, s2a *s2b; Neoconocephalus triops* (L.) 2-N, *s2a* s2b; *Neoconocephalus caudellianus* (Davis) ?-A, s2a; *Orchelimum agile* (DeGeer) 2-A, s2a; *Orchelimum pulchellum* Davis 2-N, s2a; *Nemobius fasciatus socius* Scudder 2-C, s1a; *Nemobius ambitiosus* Scudder 2-N, s1a; *Hapithus brevipennis* Saussure 2-N, *s2a* s2b.

Infrequent: *Doru lineare* (Eschscholtz) 1-N, s2a; *Ischnoptera deropeltiformis* (Brunner) 1-C, s1a *s2a; Stagmomantis floridensis* Davis 1-A, s2a; *Neotettix bolteri* Hancock 1-A, s1a; *Metaleptea brevicornis* (L.) 1-A, s2a; *Syrbula admirabilis* (Uhler) 1-N, *s2a* s2b;

Clinocephalus elegans 1-N, s1a *s2a; Arphia granulata* Saussure 1-F, *s1a* s2a; *Romalea microptera* (Beauvois) 1-N, s1a; *Opshomala vitreipennis* (Marschall) 1-C, s2a; *Leptysma marginicollis* (Serville) 1-C, s2a; *Schistocerca alutacea* form *alutacea* (Harris) 1-N, s2a; *Gymnoscirtetes pusillus* Scudder 1-C, s2a; *Melanoplus* sp. (Clypeatus Group) 1-C, s2a; *Paroxya clavuliger* (Serville) 1-C, s2a; *Scudderia cuneata* Morse 1-A, s2a; *Amblycorypha floridana carinata* Rehn & Hebard 1-A, s2a *s2b; Amblycorypha uhleri* Stal 1-F, s2a; *Belocephalus subapterus subapterus* Scudder 1-F, s1a *s2a s2b; Conocephalus gracillimus* (Morse) 1-A, s2a; *Conocephalus brevipennis* (Scudder) 1-A, s2a *s2b; Anaxipha exigua* (Say) 1-A, s2a; *Anaxipha delicatula* (Scudder) 1-A, s2a; *Anaxipha pulicaria* (Burmeister) 1-F, s2a; *Falcicula hebardi* Rehn 1-N, s2a; *Phyllopalpus pulchellus* Uhler 1-N, s2a.

The species assemblage found in this habitat shows a close affinity with that of the Pond Margin Habitat. This is due chiefly to the similarity in herbaceous plant growth and soil-water relations. The orthopteran assemblage in the Moist, Ruderal Grassland Habitat is less stable, however, than the assemblage in the Pond Margin Habitat because more types of vegetational complexes are included within the habitat. The slightly longer list of species found in the grasslands than around the pond margins is largely because of this fact.

POND MARGIN HABITAT

By far the greatest number of the ponds on the reserve are of the fluctuating type. Most of them have gently sloping banks and slight fluctuations in the water level cause the water to advance and recede around the margins over a rather wide zone, varying in width from a few feet to twenty yards or more.

This marginal zone is occupied by an herbaceous growth which is dominated by grasses (Fig. 9). The pond margins are either treeless or there may be a few scattered second-growth slash pines. During wet weather, when the margins may be flooded, quick growing aquatic vegetation is able to get a start and partly replace the normal herbage. The number of herbs found in this habitat is very great, and there seems to be considerable variation in the occurrence of many of them from pond to pond. However, there are two more or less characteristic vegetational aggregations which form this habitat on the reserve. One type is dominated by *Spartina bakeri* Merr. This grass forms large stools or clumps, and many of these may coalesce to form large patches or rows which occupy the greater portion of the marginal zone. Other grasses which form a large part of this aggregation are *Panicum hemitomon* Schult., *Amphicarpum muhlenbergianum* (Schulte.) Hitchc., and *Fuirena scirpoidea* Michx. Beneath these taller herbs *Xeris* spp., *Rynchospora* spp., *Juncus* spp., *Centella repanda* (Pers.) Small, *Hydrocotyle* spp., and *Lycopodium* spp. are common.

The other type of vegetational aggregation occupying the marginal zone around the ponds is dominated

FIG. 9. Pond Margin Habitat. East side of pond 5. *Spartina bakeri, Andropogon* spp., and *Panicum hemitomon* are the dominants in the herbaceous stratum. At the left center is the vegetation in the open water of the Pond Habitat where *Castalia lekophylla* and *Panicum hemitomon* are the common plants. September 26, 1940.

by the broom sedges *Andropogon brachystachys* Chapm. and *Andropogon capillipes* Nash. A large number of other herbs are found growing among these dominants but the most common are *Panicum leucothrix* Nash, *Panicum wrightianum* Scribn., *Rhexia Nashii* Small, *Axonopus furcatus* (Flugge) Hitchc., *Scleria* spp., *Centella repanda* (Pers.) Small, *Lycopodium adpressum* (Chapm.) Lloyd & Undw., *Ludwigia suffruticosa* Walt., *Eupatorium* spp., and *Pluchea* spp.

A dense growth of saw palmettos is usually found to form a ring or ballustrade between the flatwoods and the herbaceous marginal growth. The palmettos, which are usually in a pure stand, occupy the zone which is kept moist by the seepage water from the flatwoods. Laessle (1942) has pointed out that, in general, saw palmettos grow most luxuriantly on soil which is kept in a nearly saturated condition by seepage water from higher ground levels.

The strata which are recognizable in this habitat are (1) the hypogeic stratum; (2) the terrestrial stratum, which is made up of three ecological niches, (2a) the bare, medium moist soil and the ground beneath the vegetation, (2b) the leaf mold on the ground, and (2c) the low, mat grasses which cover irregular patches on the slight depressions and some-

times near the edge of the water in the pond; and (3) the herbaceous stratum.

Forty-seven species of Orthoptera form the assemblage found here, and their relationships to the habitat are as follows:

Dominant: *Thesprotia graminis* (Scudder) 3-C, s2a *s3; Nomotettix cristatus floridanus* Hancock 4-A, *s2a* s2c; *Tettigidea lateralis lateralis* (Say) 4-A, *s2a* s2c; *Radinotatum carinatum carinatum* (F. Walker) 4-A, s2a *s3; Dichromorpha viridis* (Scudder) 3-A, s2a *s3; Opshomala vitreipennis* (Marschall) 3-A, s3; *Leptysma marginicollis* (Serville) 4-A, s3; *Gymnoscirtetes pusillus* Scudder 4-C, s3; *Eotettix signatus* Scudder 4-A, s3; *Paroxya atlantica atlantica* Scudder 4-A, s3; *Aptenopedes sphenarioides appalachee* Hebard 4-A, s3; *Odontoxiphidium apterum* Morse 4-C, s3; *Nemobius fasciatus socius* Scudder 4-A, *s2a* s3; *Nemobius ambitiosus* Scudder 4-C, s2a; *Falcicula hebardi* Rehn 3-A, s3.

Frequent: *Amblytropidia occidentalis* (Saussure) 3-N, s3; *Schistocerca americana americana* (Drury) 3-N, s3.

Occasional: *Cariblatta lutea minima* Hebard 2-N, s2b; *Ischnoptera deropeltiformis* (Brunner) 2-C, s2a *s3; Mermeria intertexta* Scudder 2-C, s3; *Schistocerca alutacea* form *alutacea* (Harris) 2-C, s3; *Schistocerca damnifica calidior* Rehn & Hebard 2-F, s3; *Belocephalus subapterus subapterus* Scudder 2-N, s2a *s3; Neoconocephalus triops* (L.) 2-C, s3; *Nemobius cubensis cubensis* Saussure 2-A, s2a; *Nemobius carolinus carolinus* Scudder 2-C, s2a; *Anaxipha pulicaria* (Burmeister) 2-F, s3; *Tridactylus minutus* Scudder 2-A, *s1* s2a.

Infrequent: *Cariblatta lutea lutea* (Saussure & Zehntner) 1-N, s2a *s2b; Stagmomantis carolina* (Johannson) 1-N, s3; *Oligonicella scudderi* (Saussure) 1-N, s3; *Anisomorpha buprestoides* (Stoll) 1-N, s3; *Paratettix rugosus* (Scudder) 1-F, s2a; *Orphulella pelidna pelidna* (Burmeister) 1-C, s2a *s2c s3; Clinocephalus elegans* Morse 1-C, s2a *s2c s3; Paroxya clavuliger* (Serville) 1-F, s3; *Scudderia cuneata* Morse 1-F, s3; *Bucrates malivolans* (Scudder) 1-N, s3; *Orchelimum agile* (DeGeer) 1-C, s3; *Orchelimum militare* Rehn & Hebard 1-F, s3; *Ceuthophilus walkeri* Hubbell 1-F, *s1* s2a; *Gryllulus assimilis* (Fabricius) 1-F, *s2b* s3; *Miogryllus verticalis* (Serville) 1-F, *s2a* s3; *Anaxipha scia* Hebard 1-A, s3; *Gryllotalpa hexadactyla* Perty 1-F, *s1* s2a; *Scapteriscus acletus* Rehn & Hebard 1-A, *s1* s2a; *Tridactylus apicialis* Say 1-A, *s1* s2a.

MARGINAL THICKET HABITAT

As the name suggests, this habitat usually does not form on extensive horizontal areas, but it is generally found as an outer border to the bayhead type of vegetation (Fig. 14). Sometimes, however, it forms narrow, winding rows along low channels throughout the slash pine flatwoods, or occurs as narrow strips between the flatwoods and the hammocks along the river. This vegetational type is a successional stage formed when fires have been kept out of the slash pine flatwoods and from the marginal thickets.

While slash pines are usually present as the dominant tree growth, they may be interspersed with *Pinus serotina* Michx. or the tree growth may be entirely lacking. When the tree stratum is present it is a continuation of that stratum from the slash pine flatwoods.

The shrubs, which form such a conspicuous feature of this habitat, are usually from five to seven feet tall and are so densely spaced that the habitat is almost impenetrable, especially when around the margins of the bayheads. The outer edge is composed of a dense growth of *Ilex glabra* (L.) A. Gray mixed with *Aronia arbutifolia* (L.) Ell. Toward the bayhead vegetation, or toward the center of this habitat when it is not marginal, the luxuriant growth consists of *Cerothamnus ceriferus* (L.) Small, *Rubus betulifolius* Small, and some *Aronia arbutifolia*. Over these shrubs there is usually a thick tangle of *Smilax laurifolia* L. and *Muscadina munsoniana* (Simpson) Small. Beneath the higher shrubbery is a very heavy growth of *Serenoa repens* (Bartr.) Small, the trunks of which are often exposed for a foot or more below the bases of the fronds and about which leaves and mosses accumulate.

In the more moist portions Sphagnum moss covers large patches of the ground, and above the moss extends the fronds of *Osmunda cinnamomea* L. and *Anchistea virginica* (L.) Presl.

The three recognizable strata in this habitat are (1) the hypogeic stratum, (2) the terrestrial stratum which consists of the accumulated leaf mold and debris beneath the heavy vegetation, and (3) the shrub stratum.

Twenty-three species of Orthoptera are found within the Marginal Thicket Habitat. They may be divided into the following categories with respect to their frequency, abundance, and the strata which they occupy:

Dominant: *Tettigidea lateralis lateralis* (Say) 3-C, s2; *Schistocerca alutacea* form *alutacea* (Harris) 4-C, s3; *Melanoplus* sp. (Clypeatus Group) 4-A, s3; *Scudderia cuneata* Morse 4-A, s3; *Phyllopalpus pulchellus* Uhler 3-A, s3; *Gryllotalpa hexadactyla* Perty 3-A, *s1* s2.

Frequent: *Odontoxiphidium apterum* Morse 3-F, s3.

Occasional: *Anisomorpha buprestoides* (Stoll) 2-A, s3; *Aptenopedes sphenarioides appalachee* Hebard 2-N, s3; *Aptenopedes aptera saturiba* Hebard 2-N, s3; *Nemobius ambitiosus* Scudder 2-F, s2.

Infrequent: *Thesprotia graminis* (Scudder) 1-N, s3; *Mermeria intertexta* Scudder 1-N, s3; *Clinocephalus elegans* Morse 1-N, s2 *s3; Schistocerca obscura* (Fabricius) 1-A, s3; *Eotettix signatus* Scudder 1-C, s3; *Paroxya atlantica atlantica* Scudder 1-C, s3; *Scudderia curvicauda laticauda* Brunner 1-N, s3; *Amblycorypha floridana floridana* Rehn & Hebard 1-N, s3; *Amblycorypha floridana carinata* Rehn & Hebard 1-N, s3; *Orchelimum glaberrimum* (Burmeister) 1-F, s3; *Anaxipha pulicaria* (Burmeister) 1-F, s3; *Hapithus brevipennis* Saussure 1-N, s3.

The Marginal Thicket Habitat is not sharply de-

fined from the other poorly drained and meso-hydric associations in having a large number of orthopteran species confined to it, but it has many species common to all of them. The assemblage appears to be closely allied with that of the flatwoods group of habitats, with the exception of the Shrubby, Longleaf Pine Flatwoods Habitat, and it is also very similar to those found in the Pond Margin and the Moist, Ruderal Grassland Habitats. A study of the percentage composition, however, indicates that there is considerable difference between the Marginal Thicket Habitat and the others.

Two orthopteran species are particularly characteristic of this habitat and appear to be diagnostic of this type of environment. These are *Melanoplus* sp. (Clypeatus Group) and *Scudderia cuneata*.

Other distinctive characters are the presence of *Schistocerca obscura* with greater abundance than in any other habitat, and with the exception of a few individuals found in the Mesic Hammock Habitat, this was the only place it was found; the presence of *Schistocerca alutacea* form *alutacea* with a very high frequency; the high frequency of occurrence and abundance of *Phyllopalpus pulchellus*, the presence in numbers being correlated with the heavy growth of saw palmetto with which this species has been found to be associated in a high degree; and the high frequency and abundance of *Gryllotalpa hexadactyla*.

LONGLEAF PINE FLATWOODS HABITAT

Most of the areas throughout northern Florida having soils of the Leon series support a type of vegetation known as "longleaf pine flatwoods". The dominant tree is the longleaf pine, *Pinus australis* Michx., sometimes occurring in fairly dense stands with little undergrowth, but much more frequently and typically in open stands with a variably dense and characteristic undergrowth. All of the longleaf pine flatwoods on the reserve are of this more open type (Fig. 10). Fire is always an important factor in this environment, retarding succession, maintaining the vegetational type, and preventing the establishment of other tree species. It is, for example, responsible for the absence of slash pine which is much less resistant to fire than the longleaf. It is also an aid to the germination of the seeds of the latter species.

Two stages in the fire succession in longleaf pine flatwoods may be recognized, each of which constitutes a distinct habitat from the standpoint of their orthopteran inhabitants. Following recent fires, and of indefinite persistence, so long as fires recur at fairly frequent intervals, is an early successional stage characterized by the presence of abundant wire grass and herbage in addition to the shrubbery that occurs in all longleaf pine flatwoods. Since recurrent fires are the rule rather than the exception, this stage is of much more frequent and widespread occurrence than the later ones, and the term "longleaf pine flatwoods" is here restricted to this typical phase of the vegetational complex. If fire is kept out for fairly long periods, as has been the case for six to eight years on parts of the reserve, the shrubby undergrowth becomes denser and taller, and in time more or less completely crowds out the herbaceous stratum. Elimination of the grass and herbage-filled openings results in the disappearance of a considerable number of orthopteran species present in the earlier stages, and this creates a different orthopteran environment, the Shrubby, Longleaf Pine Flatwoods Habitat, which is separately treated later.

FIG. 10. Longleaf Pine Flatwoods Habitat. Looking toward the fire tower from trail 9. The typical herbaceous and shrub undergrowth, consisting dominantly of wire grasses, fetterbush, gallberry, and saw palmetto, is shown. The tall feathery-looking grass is *Sorghastrum secundum*, a characteristic fall grass in this type of flatwoods. September 26, 1940.

Although the longleaf pine flatwoods are somewhat higher and better drained than the other flatwoods types, they exhibit the peculiar water relations consequent upon level topography, high average water table, and presence of a hardpan layer which were mentioned in the general discussion of the associations occurring in poorly drained situations. The hardpan lies at a depth of two to four feet in the longleaf pine flatwoods of the reserve. During periods of wet weather the soil above this layer is often saturated, but it tends to dry out readily, and in times of drought this upper soil zone may become extremely dry even though the soil below the hardpan may still be saturated. As a result of this and the acid nature of the soil, the vegetation is rather markedly xerophytic in composition in the typical portions of the habitat.

The shrubs most characteristic of the typical longleaf pine flatwoods are saw palmetto, which does not usually attain a height of more than three feet in this environment, *Desmothamnus lucidus* (Lam.) Small, *Xolisma fruticosa* (Michx.) Small, *Quercus minima* (Sarg.) Small, *Befaria racemosa* Vent., *Cyanococcus myrsinites* (Lam.) Small, *Lasiococcus dumosus* (Andr.) Small, *Ilex glabra* (L.) A. Gray, and *Kalmiella hirsuta* (Walt.) Small. The herbaceous undergrowth consists largely of *Aristida stricta* Michx., *Sorghastrum secundum* (Ell.) Nash, *Seriocarpus bifoliatus* (Walt.) Porter, *Aster walteri* Alexander, *Aureolaria pectinata* (Nutt.) Pennell, *Sabbatia elliottii* Steud., *Hypoxis juncea* J. E. Smith, *Crotalaria rotundifolia* (Walt.) Poir., *Pilostaxis nana* (Michx.) Raf., and *Agalina* spp. Beneath the taller herbs, and often forming a discontinuous mat over the surface of the ground, are a large number of smaller herbs, among which may be noted the rosettes of young *Trilisa odoratissima* (Walt.) Cass, low species of *Panicum*, and some lichens and mosses. Under the denser shrubbery and herbage, a thin layer of leaves and other debris covers the ground.

Severe fires in this habitat clean out most of the undergrowth and destroy accumulations of debris, leaving the ground nearly bare and the larger shrubs apparently dead. This condition is only temporary, however, for most of the flatwoods plants have underground roots and stems from which new shoots soon arise. The fires open the undergrowth sufficiently to enable various small annuals and biennials to gain a foothold, and such herbaceous perennials as wire grass to maintain themselves.

The number of orthopteran species present in the typical phase of the longleaf pine flatwoods is unusually large, and it is noteworthy that the degree of overlap with the faunas of other habitats is greater than in the instance of any of the other habitats represented on the reserve. To a large degree this reflects the extent to which minor habitats, also present in other major habitats, are represented in the longleaf pine flatwoods. In part, however, it results from another complicating factor. This is the presence of small patches of atypical environment within areas of typical flatwoods. Some spots are a little lower and wetter or a little higher and better drained than the rest, yet not sufficiently extensive to constitute separate habitat areas. This situation is, of course, not unique for the flatwoods, and enters into all of the habitats to some degree, but it is particularly marked in the longleaf pine flatwoods. For mobile animals, such as Orthoptera, the small size of these areas makes them an integral part of the general environment, and it is, in part, the variety introduced into the habitats by these occurrences that accounts for the degree of overlapping observed in the orthopteran faunas of the different habitats.

In the instance of the present habitat, certain low and relatively moist spots have been included which, from the standpoint of a plant ecologist, might be treated as enclosed areas of slash pine flatwoods. These cannot thus be considered with respect to the Orthoptera. In one such place, where trail 7 cuts through a small area of low ground, water stood upon the surface in periods of wet weather, and the mat grass, *Eleocharis baldwinii* (Torr.) Chapm., formed a dense growth along and in the trail. Here also occurred *Hypericum galioides* Lam., *Drosera brevifolia* Pursh, and *Syngonanthus flavidulus* (Michx.) Ruhl, all of which plants are quite characteristic of the slash pine flatwoods but not of typical longleaf pine flatwoods. This area was of particular interest because of the seasonal relations of *Orphulella pelidna pelidna* in it and in the surrounding higher locations.

Forty-nine species form the assemblage of Orthoptera found in this habitat. They occupy four recognizable strata as follows: (1) hypogeic stratum; (2) terrestrial stratum, which may be divided into three ecological niches, (2a) the bare soil and ground beneath the vegetation, (2b) the low mat grass growing over the surface of the soil in slightly more moist places, (2c) the accumulated leaves and other debris, and decaying wood on the floor of the flatwoods; (3) herbaceous and shrub stratum, which is composed of (3a) the herbaceous minor habitat, and (3b) the shrub minor habitat; (4) the coniferous arboreal stratum, which consists of (4a) the tree trunks, and (4b) the tree crowns as places of occupancy for the Orthoptera of this stratum.

Dominant: *Prolabia pulchella* (Serville) 4-A, s2c; *Anisomorpha buprestoides* (Stoll) 4-A, s3a *s3b; Nomotettix cristatus floridanus* Hancock 4-C, *s2a* s2b; *Neotettix femoratus* (Scudder) 4-A, *s2a* s2b; *Radinotatum carinatum carinatum* (F. Walker) 4-A, s2a *s3a; Mermeria intertexta* Scudder 4-A, s3a; *Syrbula admirabilis* (Uhler) 3-A, s3a; *Schistocerca americana americana* (Drury) 3-C, s3a *s3b s4a; Gymnoscirtetes pusillus* Scudder 4-A, s3a; *Aptenopedes sphenarioides appalachee* Hebard 4-C, *s3a* s3b; *Belocephalus subapterus subapterus* Scudder 4-C, *s2a* s3a s3b; *Neoconocephalus triops* (L.) 4-C, *s2a s3b* s4b; *Orchelimum minor* Bruner 4-A, s4b; *Odontoxiphidium apterum* Morse 4-A, s2a *s3a* s3b; *Miogryllus verticalis* (Serville) 4-A, *s2a s2b* s3a; *Nemobius ambitiosus* Scudder 4-A, *s2a* s2b; *Anaxipha pulicaria* (Burmeister) 3-C, s2a *s2b; Falcicula hebardi* Rehn 3-A, s3a.

Frequent: *Cariblatta lutea lutea* (Saussure & Zehntner) 3-N, s2a *s2c; Amblytropidia occidentalis* (Saussure) 4-N, *s3a* s3b; *Arphia granulata* Saussure 3-N, *s2a s2b* s3a; *Paroxya atlantica atlantica* Scudder 3-N, s3a; *Aptenopedes aptera saturiba* Hebard 3-N, s2a *s3a s3b; Hapithus brevipennis* Saussure 3-N, s3a *s3b*.

Occasional: *Cariblatta lutea minima* Hebard 2-C, s2a *s2c; Stagmomantis carolina* (Johannson) 2-A, s3a *s3b; Thesprotia graminis* (Scudder) 2-F, *s3a* s3b; *Schistocerca alutacea* form *rubiginosa* Scudder 2-F, s3a *s3b; Scudderia texensis* Saussure & Pictet 2-F, *s3a* s3b; *Neoconocephalus robustus crepitans* (Scudder) 2-N, *s3a* s3b; *Ceuthophilus latibuli* Scudder 2-F, *s1* s2a; *Gryllulus assimilis* (Fabricius) 2-C, *s2c* s3a.

Infrequent: *Ischnoptera deropeltiformis* (Brunner) 1-N, *s2a* s3a; *Parcoblatta fulvescens* (Saussure & Zehntner) 1-N, *s2c* s3a s3b; *Arenivaga floridensis* Caudell 1-A, s2a; *Manomera brachypyga* Rehn & Hebard 1-N, s3b; *Tettigidea lateralis lateralis* (Say) 1-N, *s2a* s2b; *Mermeria picta* (F. Walker) 1-F, s3a; *Orphulella pelidna pelidna* (Burmeister) 1-C, s2a *s2b; Clinocephalus elegans* Morse 1-C, s2a *s2b s3a; Eotettix signatus* Scudder 1-N, s3a; *Melanoplus adelogyrus* Hubbell 1-F, s2a *s3b; Melanoplus femurrubrum propinquus* Scudder 1-F, s2a *s3a; Melanoplus keeleri keeleri* (Thomas) 1-C, *s3a* s3b; *Scudderia curvicauda laticauda* Brunner 1-A, *s3a* s3b; *Neoconocephalus velox* Rehn & Hebard 1-N, *s3a* s3b; *Orchelimum glaberrimum* (Burmeister) 1-F, s3a; *Nemobius fasciatus socius* Scudder 1-N, *s2a* s3a; *Cycloptilum bidens* Hebard 1-F, s2c.

Shrubby, Longleaf Pine Flatwoods Habitat

As was stated under the discussion of the last habitat, fires in the longleaf pine flatwoods open up the undergrowth sufficiently for annuals and biennials to invade such a situation. This is a temporary condition, for the normal plants of this type of flatwoods have underground roots and stems from which new vegetation soon springs after a burn. If fire is prevented for a sufficient length of time, the shrubby growth, which comes to dominate the grasses and forbs, will drive the latter out, and the undergrowth of the flatwoods becomes almost entirely shrubby.

Such a longleaf pine flatwoods is different from the more grassy type in the total assemblage of Orthoptera and also in the percentage composition of the different species which may be common to both types. This is in part due to the differences in dominant growth forms of the undergrowth in the two types, the shrubby type bringing in more thamnophilous species and hindering herbage-loving species from entering, and it is also due to the differences which the two types produce in humidity, ground cover, etc.

The shrubby type of longleaf pine flatwoods shows all gradations from slightly grassy to completely shrubby, but, in general, the following are characteristic: the shrubby growth is more open, permitting more sunlight to penetrate to the ground than in the grassy, longleaf pine flatwoods, and this prevents the growth of many kinds of mosses and smaller herbs which are found in the latter because of the lowered humidity and increase in light and air currents; the ground is covered with a thicker layer of leaves from the shrubs, and this affords a better habitat for certain roaches and crickets.

Thirty-three species of Orthoptera have been found to live in this habitat, occupying three definite strata which are (1) the terrestrial stratum, consisting of the accumulated dead leaves from the shrubs and the rather small areas of bare soil (the bare soil has not been considered a distinct ecological niche in the case of this habitat because of the very small patches which are not covered by leaves); (2) the herbage and shrub stratum, further divided into (2a) the poorly developed herbaceous minor habitat, and (2b) the shrub minor habitat; (3) the coniferous arboreal stratum, made up of (3a) the tree trunks and (3b) the tree crowns.

Dominant: *Syrbula admirabilis* (Uhler) 3-A, s2a *s2b; Amblytropidia occidentalis* (Saussure) 4-N, s2a; *Arphia granulata* Saussure 3-C, s1; *Gymnoscirtetes pusillus* Scudder 4-C, *s2a* s2b; *Aptenopedes aptera saturiba* Hebard 4-A, s2a *s2b; Odontoxiphidium apterum* Morse 4-C, s1 *s2a* s2b; *Nemobius ambitiosus* Scudder 4-C, *s1* s2a; *Hapithus brevipennis* Saussure 4-C, s2a *s2b*.

Frequent: *Thesprotia graminis* (Scudder) 3-N, s2a; *Neotettix femoratus* (Scudder) 3-N, s1; *Radinotatum carinatum carinatum* (F. Walker) 3-N, *s2a* s2b; *Orphulella pelidna pelidna* (Burmeister) 4-F, s2a; *Schistocerca americana americana* (Drury) 3-N, s2b; *Melanoplus adelogyrus* Hubbell 3-N, s2b; *Atlanticus gibbosus* Scudder 3-N, s2b.

Occasional: *Cariblatta lutea lutea* (Saussure & Zehntner) 2-F, s1; *Mermeria picta* (F. Walker) 2-N, *s2a* s2b; *Schistocerca alutacea* form *rubiginosa* Scudder 2-F, s2a *s2b; Schistocerca damnifica calidior* Rehn & Hebard 2-N, s2b; *Melanoplus keeleri keeleri* (Thomas) 2-N, s2a *s2b; Scudderia texensis* Saussure & Pictet 2-C, s2a *s2b; Orchelimum minor* Bruner 2-A, s3b; *Ceuthophilus latibuli* Scudder 2-N, s1.

Infrequent: *Prolabia pulchella* (Serville) 1-A, s1; *Ischnoptera deropeltiformis* (Brunner) 1-F, s1; *Anisomorpha buprestoides* (Stoll) 1-N, s2b; *Nomotettix cristatus floridanus* Hancock 1-F, s1; *Tettigidea lateralis lateralis* (Say) 1-F, s1; *Paroxya atlantica atlantica* Scudder 1-F, s2a; *Aptenopedes sphenarioides appalachee* Hebard 1-F, s2a *s2b; Belocephalus subapterus subapterus* Scudder 1-N, s2b; *Gryllulus assimilis* (Fabricius) 1-F, s1; *Falcicula hebardi* Rehn 1-F, s2b.

Black Pine Flatwoods Habitat

The type of flatwoods which forms this habitat is found on St. Johns fine sand. The very flat areas on the reserve upon which this soil type occur are at slightly lower elevations than those occupied by Leon fine sand, and water usually stands for a longer period in the wet season. This soil, as previously pointed out, has a hard layer of sand mixed with organic matter at the surface. At depths varying from two to four feet another organic hardpan is found. This factor, as well as others caused by it, and the extreme flatness of areas on which St. Johns soils occur probably play the greatest role in determining the vegetation of this type of flatwoods. Laessle (*op. cit.*, p. 47) has suggested the following causes for the relatively poor vegetational growth on this soil: the hard organic surface layer undoubtedly prevents many plants from becoming established; the St. Johns soil, because it is lower than Leon soil, has water standing over it for a longer period of time; the hard organic layer on top may prevent sufficient aeration of the soil beneath; the flatness of these areas prevents much lateral movement of the

soil water which would allow toxic substances to accumulate and prevent the establishment of plants which are not tolerant to these toxins.

As the name of this habitat suggests, the dominant tree growth is black pine, *Pinus serotina* Michx. The stands of this pine are always very open, with only a few trees scattered over the entire habitat. In some areas, pines are entirely lacking. A few longleaf and slash pines may be found along with the black pine (Fig. 11).

The undergrowth is almost exclusively shrubby, and almost entirely composed on *Desmothamnus lucidus* (Lam.) Small. *Xolisma fruticosa* (Michx.) Small, *Ilex glabra* (L.) A. Gray, *Kalmiella hirsuta* (Walt.) Small may occur, thinly scattered, among the fetterbush. A few *Serenoa repens* (Bartr.) Small are also thinly scattered, and in this situation extremely dwarfed, rarely reaching a height of over one foot.

The extremely scant herbaceous growth consists of *Aristida spiciformis* Ell., which seems to be diagnostic of this type of flatwoods, *Andropogon brachystachys* Chapm., *Andropogon capillipes* Nash, and very rarely *Aristida stricta* Michx., and *Sorghastrum secundum* (Ell.) Nash, both of which are very common in the longleaf pine flatwoods.

The three strata in which the species occur are (1) the terrestrial stratum which consists of the bare

FIG. 11. Black Pine Flatwoods Habitat. Flatwoods northeast of the junction of trails 6 and 8. The pines are relatively few in number in this type of flatwoods on the reserve. The heavy growth of *Desmothamnus lucidus* forms practically the entire undergrowth. Saw palmettos are extremely dwarfed when growing on St. Johns soil. September 26, 1940.

soil and ground beneath the vegetation; (2) the herbage and shrub stratum, made up of the (2a) herbaceous and (2b) shrub minor habitats and (3) the coniferous arboreal stratum, in which the species may occur on (3a) the tree trunks or (3b) the tree crowns.

The distribution of the twenty-nine species of Orthoptera found in this habitat and their quantitative relations are as follows:

Dominant: *Anisomorpha buprestoides* (Stoll) 4-C, *s2a* s2b; *Neotettix femoratus* (Scudder) 3-C, s1; *Amblytropidia occidentalis* (Saussure) 4-C, s2a; *Schistocerca americana americana* (Drury) 3-C, s2a *s2b s3a; Gymnoscirtetes pusillus* Scudder 4-C, *s2a* s2b; *Aptenopedes aptera saturiba* Hebard 3-C, s2a *s2b; Odontoxiphidium apterum* Morse 4-C, *s1* s2a *s2b; Nemobius ambitiosus* Scudder 4-C, s1; *Hapithus brevipennis* Saussure 4-A, s2a *s2b*.

Frequent: *Thesprotia graminis* (Scudder) 3-N, *s2a* s2b; *Radinotatum carinatum carinatum* (F. Walker) 3-N, s1 *s2a; Syrbula admirabilis* (Uhler) 3-N, s2a; *Arphia granulata* Saussure 3-N, *s1* s2b.

Occasional: *Nomotettix cristatus floridanus* Hancock 2-C, s1; *Mermeria intertexta* Scudder 2-N, *s2a* s2b; *Orphulella pelidna pelidna* (Burmeister) 2-F, s1 *s2b; Schistocerca alutacea* form *rubiginosa* Scudder 2-F, s1 *s2b; Schistocerca damnifica calidior* Rehn & Hebard 2-F, s2b.

Infrequent: *Cariblatta lutea lutea* (Saussure & Zehntner) 1-F, s2a; *Oligonicella scudderi* (Saussure) 1-A, s2a; *Mantoida maya* Saussure & Zehntner 1-N, s2a *s2b; Tettigidea lateralis lateralis* (Say) 1-N, s1; *Mermeria picta* (F. Walker) 1-F, s2a *s2b; Clinocephalus elegans* Morse 1-F, s1; *Aptenopedes sphenarioides appalachee* Hebard 1-F, s2a *s2b; Scudderia curvicauda laticauda* Brunner 1-N, s2b; *Amblycorypha floridana carinata* Rehn & Hebard 1-F, s2a *s2b; Belocephalus subapterus subapterus* Scudder 1-C, s1 *s2b; Falcicula hebardi* Rehn 1-N, *s2a* s2b.

SLASH PINE FLATWOODS HABITAT

Unlike the longleaf pine and the black pine flatwoods, the slash pine flatwoods are found on Plummer or Portsmouth fine sand. These do not have a hardpan layer. They are at a lower elevation than the St. Johns and Leon, and, consequently, the subsoil is generally wet for most of the year and there is a considerable amount of organic matter accumulated in the upper horizons.

Slash pine, *Pinus palustris* Mill., is the dominant tree growth, but longleaf and black pine may be interspersed in varying degrees, depending upon the frequency of fire and cutting. These two factors also have a marked effect upon the undergrowth. Frequent fires produce an undergrowth which is predominantly herbaceous, very luxuriant and dense. The bunch grasses, *Andropogon capillipes* Nash, *Andropogon brachystachys* Chapm., and *Andropogon perangustatus* Nash, are very abundant (Fig. 12). The wire grasses are common and may reach a height of two or more feet. Shrubs are also present in this grassy type, and although they may be locally dominant they are not dominant in respect to this vege-

FIG. 12. Slash Pine Flatwoods Habitat. This is a grassy type of slash pine flatwoods south of pond 2.

tational association as a whole. The common shrubs are saw palmetto, which may form large clumps or long winding rows through the flatwoods, gallberry, and fetterbush.

The slash pine flatwoods have a more shrubby undergrowth when fires have been kept out, and the understory begins to approach the bayhead type of vegetation. This more shrubby type is common about the margins of bayheads, and it may form long, winding or labyrinthic courses along small water channels. These latter are a distinct habitat which has been discussed as the Marginal Thicket Habitat.

The orthopteran assemblage is distributed in three well-marked strata within the major habitat. These are (1) the terrestrial stratum, formed by the bare sand and bare soil beneath vegetation; (2) the herbaceous and shrub stratum, which may be divided into the component parts, (2a) herbage and (2b) shrubbery; and (3) the coniferous arboreal stratum, consisting of the slash pine tree crowns.

The orthopteran species which occupy this habitat, and their relative frequencies and abundance are given below.

Dominant: *Radinotatum carinatum carinatum* (F. Walker) 4-A, s1 *s2a; Mermeria intertexta* Scudder 3-A, *s2a* s2b; *Gymnoscirtetes pusillus* Scudder 4-C, s2a; *Aptenopedes sphenarioides appalachee* Hebard 3-A, *s2a* s2b; *Orchelimum glaberrimum* (Burmeister) 4-A, s2a.

Frequent: *Cariblatta lutea lutea* (Saussure & Zehntner) 3-N, s1; *Paroxya atlantica atlantica* Scudder 3-N, s2a; *Scudderia cuneata* Morse 3-N, s2a; *Orchelimum minor* Bruner ?-?, s3; *Odontoxiphidium apterum* Morse 3-N, s2a *s2b; Nemobius ambitiosus* Scudder 3-N, s1.

Occasional: *Cariblatta lutea minima* Hebard 2-F, s1; *Nomotettix cristatus floridanus* Hancock 2-F, s1; *Syrbula admirabilis* (Uhler) 2-N, *s2a* s2b; *Orphulella pelidna pelidna* (Burmeister) 2-F, s1 *s2a; Falcicula hebardi* Rehn 2-C, s2a.

Infrequent: *Ischnoptera deropeltiformis* (Brunner) 1-N, s1; *Stagmomantis floridensis* Davis 1-N, s2a *s2b; Opshomala vitreipennis vitreipennis* (Marschall) 1-F, s2a; *Eotettix signatus* Scudder 1-N, s2a; *Melanoplus* sp. (Clypeatus Group) 1-F, *s2a* s2b; *Aptenopedes aptera saturiba* Hebard 1-N, s2a *s2b; Scudderia curvicauda laticauda* Brunner 1-C, s2a; *Gryllulus assimilis* (Fabricius) 1-F, s1; *Hapithus brevipennis* Saussure 1-N, s2a *s2b*.

HYDRIC ASSOCIATIONS

Three main types of natural aquatic situations occur on the reserve. These are the ponds and water courses in the flatwoods, the springs and spring runs, and the St. Johns River. From the initial aquatic vegetation in these places, two parellel lines of succession leading ultimately to hydric hammock are to be observed; namely, the pond seres and the river seres. Differences in the vegetational development in these two hydroseres are due chiefly to the differences in pH of the water in the ponds and water courses and the water of the river and springs. Beecher Spring, just south of the reserve boundary, shows successional development much like that in the ponds toward the upper end, except near the spring head where the water is flowing too fast for emergent vegetation to become established. Mud Spring, on the other hand, heads but a short distance from the river and the spring run has become a relatively wide tidal tributary of the river. The vegetational succession along the banks of the run is typically that which is found along the shores of the river.

The primary, submerged vegetational stages of both of these hydroseres are of no concern here as orthopteran habitats. The emergent stage of succession in the ponds form the first orthopteran habitat, the Pond Habitat. The early bog stage of vegetational development in the pond seres, before the growth of a shrub stratum, also is a part of this habitat. When organic matter has become thicker and the water in the ponds shallow shrubs begin to invade these situations and a bayhead vegetation develops. This stage of plant growth is the orthopteran Bayhead Habitat. The further accumulation of organic matter, along with the prevention of fires, leads to the development of the hydric hammock which forms what I have called the Low Hammock Habitat.

In the vegetational succession from priseres along the river, the mats of water hyacinths, which are part of the floating vegetation stage, form the first orthopteran habitat. This habitat, however, is not well-established nor very permanent, and it is treated separately from the other hydric environments. The marsh stages form the first well-established orthopteran habitats. When organic matter has accumulated sufficiently beneath the water, but not enough to be exposed above the water level for any length of time, the saw grass marsh develops, and this vegetational association is the orthopteran Saw Grass Marsh Habitat. With further accumulation of organic matter and a consequent higher ground level, the marsh

is not flooded permanently and *Spartina bakeri* Merr. becomes established. This marsh grass association forms the Spartina Marsh Habitat. The next stage of vegetational succession is the swamp, with deciduous trees forming the dominant plant growth. This vegetational association is the Alluvial Hammock Habitat. If organic matter accumulates in greater amount, the soil is built above a level which is subject to flooding by the river, and the hydric hammock, dominated by hardwood evergreen trees, succeeds the swamp. The hydric hammock, as already stated, forms the low Hammock Habitat for Orthoptera.

POND HABITAT

Throughout the flatwoods areas of the reserve are many scattered ponds (Fig. 9). All of them are shallow and the water in most of them fluctuates considerably throughout the seasons, for their level is influenced by run-off and seepage from the flatwoods. Some ponds, on the other hand, have little fluctuation in their water level, and these tend to have a somewhat different type of vegetation around their margins. It seems clear that the water level of many, or perhaps all of the ponds is controlled, in part, by underground drainage channels. During the spring of 1939, the ponds at the south end of the reserve were nearly dry while those at the north end were filled with water to the normal level. In the fall of 1940, beginning about the last of October, this condition was reversed. The ponds at the north end of the reserve were completely dry while those at the south end were somewhat lower than usual but had water in them. Changing underground water courses, with coalescence and stream capture of some of the channels, would account for this variation in conditions from years to year. All of these flatwoods ponds are very acid, ranging in pH from 4.0 to 5.0 (Pierce 1947) and the water in all of them is about the color of tea.

The maximum depth of the water in most of the ponds is between three and five feet. A few have been filled with organic matter until they are much shallower than this during the rainy season, and they are dry or only moist during the major part of the year. Ponds of this type are entirely occupied by *Anchistea virginica* (L.) Presl. and Sphagnum moss. The deeper ponds show definite zonation of the vegetation, the zones corresponding to increase in depth of water from the margin to the center of the pond. In the shallow margins and about the moist edges, where there is little fluctuation in water level, there is often a good growth of *Anchistea virginica* beneath which is found Sphagnum moss. A relatively narrow zone follows, made up mainly of emergent plants which grow in water up to a foot in depth. Dominant among these are *Panicum hemitomon* Schult., *Leersia hexandra* Swartz, *Manisuris tuberculosa* Nash, *Panicum tenerum* Beyr., *Rhynchospora microcephala* Britton, *Rhynchospora filifolia* Torr., *Juncus* spp., *Gyrotheca tinctoria* (Walt.) Salisb., *Pluchea foetida* (L.) D.C., *Bidens mitis* (Michx.) Sherff, *Ludwigia suffruticosa* Walt., *Eupatorium leptophyllum* D.C., *Fimbristylis autumnalis* (L.) R. & S., *Centella repanda* (Pers.) Small, and *Hydrocotyle* spp.

The next deeper zone, which occurs in water from one to three feet in depth, has a large number of submerged plants as well as emergent ones. The emergent plants are the only ones which concern us here, for they alone provide a habitat for the Orthoptera. The most common plant of this zone is *Panicum hemitomon*. Other plants are *Eleocharis equisetoides* (Ell.) Torr., *Eleocharis flaccida* (Reichenb.) Urban, *Manisuris tuberculosa*, and *Pontederia lanceolata* Nutt.

The deepest parts of the ponds toward the center are filled with floating plants such as *Castalia lekophylla* Small, *Utricularia inflata* Walt., and *Vesiculina purpurea* (Walt.) Raf. In some of the shallower ponds, *Panicum hemitomon* grows completely across the center, forming in such cases a large central stand and almost completely filling some of them.

Many variations occur from pond to pond in the width of the various zones and also in the numbers of different species of plants found in each zone. However, those plants listed and their distribution in the various zones is typical. One pond, just northeast of the administration buildings had a heavy stand of *Typha latifolia* L. growing about its southern border. In a pond northwest of the administration buildings the margin was covered by a dominant growth of *Hypericum fasciculatum* Lam. This plant is of particular interest from an orthopterological standpoint because *Inscudderia strigata* is found on it almost exclusively.

Only twelve species were found to comprise the orthopteran assemblage of this habitat and they all occupy the single stratum of emergent vegetation.

Dominant: ***Opshomala vitreipennis vitreipennis*** (Marschall) 3-A; ***Leptysma marginicollis*** (Serville) 4-A; ***Schistocerca alutacea*** form ***alutacea*** (Harris) 3-A; ***Orchelimum pulchellum*** Davis 4-A; ***Orchelimum militare*** Rehn & Hebard 4-A; ***Orchelimum bradleyi*** Rehn & Hebard 3-A.

Frequent: None.

Occasional: *Paroxya clavuliger* (Serville) 2-N.

Infrequent: *Tettigidea lateralis lateralis* (Say) 1-N; *Mermeria intertexta* Scudder 1-N; *Dichromorpha viridis* (Scudder) 1-F; *Inscudderia strigata* (Scudder) 1-A; *Orchelimum agile* (DeGeer) 1-F.

The most distinctive character of the orthopteran assemblage found in the Pond Habitat is the predominance of the genus *Orchelimum.* Four of the six species which occur on the reserve are found in this environment. *Leptysma marginicollis* and *Opshomala v. vitreipennis,* as well as *Schistocerca alutacea* form *alutacea,* are also dominant species and are highly characteristic. All of the infrequent species of the ponds, with the exception of *Inscudderia strigata,* are characteristic species of the herbaceous growths around the ponds which form the Pond Margin Habitat. *Inscudderia strigata* is found only in those ponds where the guinea cypress forms a conspicuous feature of the emergent vegetation.

SPARTINA MARSH HABITAT

All along the St. Johns River, as Harper has stated (1914), there are extensive treeless marshes which generally grade into the brackish marshes near the coast. There are three such marshy areas along the river within the boundaries of the reserve. One is located at the north end at the upper end of Little Lake George, there are extensive marshy areas running on either side of Mud Spring run and widening out from the run at various points, and the third marsh completely covers the central portion of Buzzard's Roost Point (Fig. 13). These are seasonally flooded to a depth of two or more feet, but they may be comparatively dry during the latter part of the dry season in the spring. They may be divided into two kinds from the standpoint of dominant growth, those which are dominated by the marsh grass, *Spartina bakeri* Merr., and those which are dominated by saw grass, *Mariscus jamaicensis* (Crantz.) Britton. Portions of all of these marshes may have local areas which are covered with one or the other of these plants, for saw grass usually grows in the deeper, wetter portions, while the higher spots have the marsh grass on them. The marsh at the north end of the reserve is almost entirely marsh grass, and it has been placed in the Spartina Marsh Habitat. The marshes along the Mud Spring Run are almost entirely saw grass marshes, and the large marshy area on Buzzard's Roost Point is a mixture of both.

FIG. 13. Spartina Marsh Habitat. Large marsh at the northeast corner of Buzzard's Roost. The dense mat of *Spartina bakeri* and scattered clumps of saw grass are clearly shown. One of the many thicket "islands" of shrubs and trees throughout the marsh can be seen in the background.

The Spartina Marsh Habitat is dominated by *Spartina bakeri.* Throughout this type of marsh are large open areas of water in which *Pontederia lanceolata* Nutt. and *Sagittaria lancifolia* L. are growing. Mixed with the marsh grass are the tall *Kosteletskya althaeifolia* (Chapm.) A. Gray and *Vicia floridana* S. Wats. The marsh grass grows up from large tussocks which are so closely spaced that the stalks of the grass form a very dense, almost impenetrable mass.

Higher, island-like areas throughout this type of marsh are covered by a shrubby growth. The common shrubs and small trees are *Salix longipes* Anders, *Baccharis halimifolia* L., *Cerothamnus ceriferus* (L.) Small, low-growing *Fraxinus pauciflora* Nutt., and *Rufacer rubrum* (L.) Small.

This major habitat may be divided into three strata; (1) the terrestrial stratum which consists of the accumulation of duff around the the clumps of marsh grass, and which is only present as a stratum during the dry season; (2) the *Spartina* grass and other herbage stratum, and (3) the scattered shrub stratum.

The distribution of the Orthoptera among these strata and their quantitative composition in this habitat are as follows:

Dominant: *Cariblatta lutea minima* Hebard 4-A, s1, *s2; Mermeria intertexta* Scudder 4-A, s2; *Paroxya clavuliger* (Serville) 4-A, s2.

Frequent: None.

Occasional: *Clinocephalus elegans* Morse 2-A, s2; *Schistocerca alutacea* form *alutacea* (Harris) 2-A, s2 *s3; Conocephalus aigialus* Rehn & Hebard 2-A, s2, *Nemobius carolinus carolinus* Scudder 2-N, s1.

Infrequent: *Anisomorpha buprestoides* (Stoll) 1-N, s3; *Neotettix bolteri* Hancock 1-N, s1; *Tettigidea lateralis lateralis* (Say) 1-F, s1; *Tettigidea armata* Morse 1-F, s1; *Romalea microptera* (Beauvois) 1-F, s2; *Eotettix signatus* Scudder 1-F, s2; *Neoconocephalus triops* (L.) 1-F, *s2* s3; *Anaxipha pulicaria* (Burmeister) 1-N, s2.

SAW GRASS MARSH HABITAT

The marshes along either bank of Mud Spring Run and spreading out into broad areas at various points along its course are almost entirely of this type. The marsh at the south end of the reserve on Buzzard's Roost Point has large patches of this marsh type scattered throughout, especially toward the north end and in the deeper portions near the river.

This type of habitat is composed almost entirely of the saw grass, *Mariscus jamaicensis* (Crantz.) Britton. The halbard-leaved morning glory, *Ipomoea sagittata* Cav., and *Mikania scandens* (L.) Willd. are common vines found associated with the saw grass, but little else is present except around the margins of such marshes where several distinct plants form an ecotone between the marsh and the bordering low or alluvial hammocks.

A large pond or marsh located between trails 2 and 3 near the main road through the reserve is almost completely filled with saw grass. Located as

it is, however, in a flatwoods area, the water is very acid and the other vegetation associated with the saw grass is of the flatwoods pond type.

Three strata are recognizable in this habitat. (1) The terrestrial stratum consists of the decaying vegetation on the floor of the marsh and is only present as a stratum during the dry season, (2) the saw grass stratum is predominant, and (3) the scattered shrub stratum is best developed around the periphery of the marshes and sometimes on higher ground within the marsh area.

Dominant: ***Mermeria intertexta*** Scudder 4-C, s2; ***Bucrates malivolans*** (Scudder) 3-A, s2.

Frequent: ***Cariblatta lutea minima*** Hebard 3-C, s1 *s2*.

Occasional: ***Anisomorpha buprestoides*** (Stoll) 2-A, s2 *s3*.

Infrequent: ***Eurycotis floridana*** (F. Walker) 1-F, s1 *s2*; ***Stagmomantis carolina*** (Johannson) 1-F, s2 *s3*; ***Neotettix bolteri*** Hancock 1-N, s1; ***Romalea microptera*** (Beauvois) 1-F, s2; ***Schistocerca alutacea*** form ***alutacea*** (Harris) 1-C, *s2* s3; ***Anaxipha pulicaria*** (Burmeister) 1-F, s2.

BAYHEAD HABITAT

The term "bayhead" has been used to designate several different kinds of vegetational associations by various authors. In general, the term is applied to that type of vegetation found at the upper end of small creeks or streams which are formed at places where the elevation dips below the general ground water level. The water seeps out into these depressions and flows away, and a particular type of vegetation, adapted to soil which is nearly always saturated, is to be found growing in such places. On the reserve, this type of vegetational growth is found in the depressions of the flatwoods or as marginal growths about the flatwoods ponds which do not have a noticeable variation in the water level. Laessle (1942, p. 41) has defined a bayhead as "an association dominated by broad-leaved evergreen trees that grow in very acid, saturated soils which are subject to periodic flooding." His definition is followed in this paper.

On the reserve the bayheads are found on Portsmouth fine sand over which there is usually a heavy layer of organic matter. Toward the center of the bayhead, where it is much wetter, there is usually a thick accumulation of peaty muck. Scattered, large, slash pines are usually found towering over the lower bayhead trees. These are undoubtedly relics from the previous slash pine flatwoods stage in succession. The characteristic trees of this habitat are almost exclusively different species of bay, the loblolly bay, white bay, and swamp red bay being most common. Scattered red maples and an occasional sweet gum may also be found. Beneath these trees there are a few characteristic shrubs such as *Cerothamnus ceriferus* (L.) Small and very large *Desmothamnus lucidus* (Lam.) Small which form almost impenetrable thickets near the periphery of this habitat. Over the lower shrubs and twining about the trees are *Smilax laurifolia* L. and *Muscadina munsoniana* (Simpson) Small (Fig. 14).

FIG. 14. Bayhead Habitat. Looking into a bayhead south of trail 9 at the Welaka-Georgetown road. Border of slash pines with thick undergrowth of shrubs, saw palmettos and vines form the Marginal Thicket Habitat. September, 1940.

Mounds of soil, organic matter, leaves, etc. build up around the bases of the trees to the level of a foot or more above the channels which run between and around them. These channels are usually filled with water to a depth of from eight to twleve inches, except in the winter months when the whole floor of the bayhead may be comparatively dry on the surface. The soil within the bayhead is covered with a thick carpet of leaves which is thicker in the channels than on the mounds. The upper inch or two of this leaf layer becomes dry during the dry season, but the lower layers are usually wet.

The tree growth is so dense that the interior of this habitat is excessively shaded and comparatively dark. Consequently, herbaceous vegetation is lacking. Around the borders of the bayheads, and running up into the marginal thickets, one may find the ferns *Anchistea virginica* (L.) Presl. and *Osmunda cinnamomea* L. Sphagnum moss is also found around the outer margins and in the winding and crisscrossing channels of water which traverse the bayheads.

The eleven species which make up the orthopteran assemblage found in this habitat occupy three strata; (1) the terrestrial stratum, which is composed of two ecological niches, (1a) the bare, medium-wet soil, and (1b) the leaf duff and decaying wood on the floor of the habitat; (2) the shrub stratum; and (3) the broad-leaved arboreal stratum.

Dominant: *Ischnoptera deropeltiformis* (Brunner) 3-A, s1b; *Neotettix bolteri* Hancock 3-A, *s1a* s1b; *Nemobius cubensis cubensis* Saussure 3-C, s1a *s1b; Nemobius carolinus carolinus* Scudder 4-A, s1a *s1b; Hapithus agitator quadratus* Scudder 4-A, s2.

Frequent: *Tettigidea lateralis lateralis* (Say) 3-N, *s1a* s1b.

Occasional: *Cariblatta lutea lutea* (Saussure & Zehntner) 2-F, s1b; *Anaxipha exigua* (Say) 2-A, s2.

Infrequent: *Prolabia pulchella* (Serville) 1-A, s1b; *Tettigidea armata* Morse 1-A, *s1a* s1b; *Pterophylla c. camellifolia* (Fabricius) 1-A, s2 *s3*.

The orthopteran assemblages of the tree-dominated group of hydric associations are all very similar, especially in respect to the dominant species present in each. The Bayhead Habitat contains fewer species, however, than the other two habitats in this group and the large majority of the species are found with lower frequency than in the others. This last fact seems to be correlated with the large degree of variation in the developmental growth of the vegetation in the bayheads and the consequent variation in density, the variation in thickness of ground cover, and depth of water standing on the floor of such situations.

A few of the other pertinent characteristics of the orthopteran assemblage of this habitat are the presence of *Nemobius c. carolinus* with greater abundance in this than in any of the other habitats, the presence of *Nemobius c. cubensis*, which was not found on the reserve in either the Low or Alluvial Hammock Habitats, and the absence of *Lea floridensis*, this species having been found only in the hammocks along the river. *Pterophylla c. camellifolia* has been found to be abundant in the bayheads, however, as well as in the Low and Alluvial Hammock Habitats.

Low Hammock Habitat

The low or hydric hammocks occupy a position between the mesic and the alluvial hammocks. All three of these types of hammocks grade from one to another, and often this gradation is so gradual that it is very difficult, if not impossible, to draw a definite line of demarcation between them. This is especially true of the low and alluvial hammocks. Furthermore, the low hammocks are not distinct vegetational units because they are composed of many species of plants which are common to the bayheads, river swamps, and mesic hammocks. Practically all of the low hammocks occupy a narrow belt between the river swamps and the mesic hammocks on the western side of the reserve (Fig. 15). They are found generally on Portsmouth fine sand, and they always occur on soil which is saturated or nearly saturated by run-off water from higher elevations. They are not subject, however, to the tidal and seasonal fluctuations of the river level.

The tree stratum of this habitat is composed most commonly of *Tamala pubescens* (Pursh) Small, *Quercus nigra* L., *Liquidambar styraciflua* L., *Gordonia lasianthus* (L.) Ellis, *Sabal palmetto* (Walt.) Todd, and *Ulmus floridana* Chapm. It is difficult to delimit exact vegetational strata between the upper tall tree stratum and the ground, for the smaller elements of the upper stratum, along with the various sized shrubs, fill this intervening space almost completely and in very gradual degrees. There are no sharp levels of vegetational growth.

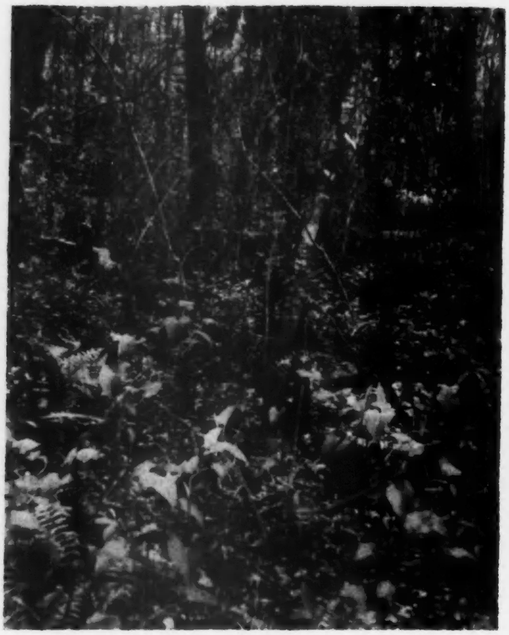


FIG. 15. Low Hammock Habitat. Low, or hydric hammock north of Buzzard's Roost Point. March 21, 1941.

The shrubs which are most common are *Ilex coriacea* (Pursh) Chapm., *Cerothamnus ceriferus* (L.) Small, *Svida microcarpa* (Nash) Small, and long rows and clumps of saw palmetto which grow to a considerable height in this habitat. Over many of the shrubs and growing around the trunks of the trees are vines of *Smilax laurifolia* L., *Smilax bona-nox* L., *Muscadina munsoniana* (Simpson) Small, *Berchemia scandens* (Hill) Trelease, *Ampelopsis arborea* (L.) Rusby, and *Toxicodendron radicans* (L.) Kuntze.

Dense shading of the ground makes it possible for only a few plants to grow in the interior of this hammock. The ferns, *Osmunda cinnamomea* L., *Osmunda regalis* L., and *Lorinseria areolata* (L.) Presl., are the most common, and on the wetter portions of this habitat may be found *Rhynchospora corniculata* (Lam.) A. Gray and Sphagnum moss.

The ground is covered with a comparatively thick layer of leaves. The lower portions of this layer are almost always wet and soggy, but the top layers dry out during the period when run-off water from higher levels is very low. Numerous rotten logs are scattered over the ground in most of the low hammocks on the reserve, and these form a rather dis-

tinct minor habitat for the rotten wood-loving Orthoptera of the major habitat.

The four strata which the twenty-six species of Orthoptera occupy are (1) the hypogeic stratum, (2) the terrestrial stratum, which is further divided into the (2a) bare, medium-wet soil and the ground beneath vegetation, and (2b) the leaf duff and decaying wood on the floor of this habitat, (3) the tall shrub stratum, and (4) the broad-leaved arboreal stratum.

Dominant: *Ischnoptera deropeltiformis* (Brunner) 4-A, s2a *s2b*; *Eurycotis floridana* (F. Walker) 4-A, s2b; *Tetrix arenosus arenosus* (Burmeister) 4-A, s2a; *Neotettix bolteri* Hancock 4-A, *s2a* s2b; *Tettigidea lateralis lateralis* (Say) 4-A, *s2a* s2b; *Romalea microptera* (Beauvois) 4-A, s2b s3; *Lea floridensis* (Beutenmuller) 4-A, s4; *Nemobius carolinus carolinus* Scudder 4-C, *s2a* s2b; *Hapithus agitator quadratus* Scudder 4-A, s3.

Frequent: *Cariblatta lutea lutea* (Saussure & Zehntner) 3-C, s2b; *Pterophylla c. camellifolia* (Fabricius) 3-N, s4.

Occasional: *Vostox brunneipennis* (Serville) 2-A, s2b; *Tettigidea armata* Morse 2-A, *s2a* s2b.

Infrequent: *Prolabia pulchella* (Serville) 1-A, s2b; *Cariblatta lutea minima* Hebard 1-F, s2b; *Parcoblatta fulvescens* (Saussure & Zehntner) 1-F, s2b; *Parcoblatta lata* (Brunner) 1-F, s2b; *Anisomorpha buprestoides* (Stoll) 1-F, s3; *Nomotettix cristatus floridanus* Hancock 1-N, *s2a* s2b; *Camptonotus carolinensis* (Gerstaecker) 1-A, *s3* s4; *Gryllulus assimilis* (Fabricius) 1-F, s2a *s2b*; *Nemobius ambitiosus* Scudder, 1-F, s2b; *Cycloptilum bidens* Hebard 1-F, s2b; *Cycloptilum trigonipalpum* Rehn & Hebard 1-N, s3; *Myrmecophila pergandei* Bruner 1-A, s1; *Gryllotalpa hexadactyla* Perty 1-A, *s1* s2a.

Thirteen of the species found in this habitat are definitely known to be present also in the Alluvial Hammock Habitat, with which the Low Hammock Habitat is closely allied. We may note these differences between the two: *Eurycotis floridana* was found only in the Low and not in the Alluvial Hammock Habitat; *Romalea microptera* and *Lea floridensis* occur here with greater frequency and abundance; *Camptonotus carolinensis*, *Cycloptilum bidens*, *Cycloptilum trigonipalpum*, and *Gryllotalpa hexadactyla* occur in this and not in the alluvial hammocks; and *Myrmecophila pergandei* was found to occur on the reserve only in the Low Hammock Habitat. This latter species is so rarely found, however, that its occurrence elsewhere could be expected.

ALLUVIAL HAMMOCK HABITAT

This type of habitat has been called "river swamp" by many authors. On the reserve, this type of hammock is found all along the St. Johns River, except on the low bluffs or slight rises in the shorelines. Such hammocks very in width, extending back from the river less than one hundred yards in places or as much as four hundred yards in others. Occasionally this fringe of hammock extends inland around the margins of the spartina and saw grass marshes which occur at frequent intervals along the river.

The areas on which this type of hammock occur are subject to the periodic fluctuation of the river level, both tidal and seasonal. The normal daily tide fluctuation at Welaka is about six inches, and since the elevation of the land on which such hammock vegetation grows is usually less than a foot above the average level of the river, this daily tidal fluctuation causes two excessive inundations of the hammocks when the river is higher than normal. The fluctuation of the level of the river from the highest during the rainy season to the lowest during the dry season is normally about two and one-half feet. This causes a submergence of the hammock floors to the greatest extent during or at the end of the rainy season, after which the hammocks become successively less and less flooded until during the winter and spring months one can easily walk to the edge of the river. However, at all times of the year the ground is always wet and becomes more and more saturated as you approach the river.

The upper vegetational stratum is composed of a rich growth of trees which extend upward to a height of from eighty to one-hundred feet, and they form a dense canopy over the lower vegetation and the ground. The dominant trees are *Taxodium distichum* (L.) L. C. Rich., *Nyssa biflora* Walt., *Gleditsia aquatica* Marsh, *Fraxinus pauciflora* Nutt., *Rufacer rubrum* (L.) Small, *Hicoria aquatica* (Michx.) Britton, and *Sabal palmetto* (Walt.) Todd. The cypress once held a higher place in the formation of the tall tree stratum than now, for large stumps stand as mute evidence of their past majesty.

Here, as in the low hammock, it is difficult to delimit exact vegetational strata between the upper tall tree stratum and the ground since there are no sharp levels of vegetational growth. Small maples, ash, honey-locusts, and sweet gums form the bulk of the stratum between the tall trees and the ground. In addition to these, characteristic shrubs are *Cephalanthus occidentalis* L., *Salix longipes* Anders, *Sabal minor* (Jacq.) Pers., and *Cerothamnus ceriferus* (L.) Small. One very noticeable feature of the small tree stratum is the dense thickets of small ash six to ten feet tall. These thickets are usually within a short distance from the river's edge. Similar thickets of very small maples, and sometimes ash, are found in scattered patches back from the river. Over these thickets, as well as over all of the lower trees and tall shrubs, and even on some of the tall trees there are vines of *Smilax bona-nox* L., *Smilax glauca* Walt., *Berchemia scandens* (Hill) Trelease, *Mikania scandens* (L.) Willd., and *Toxicodendron radicans* (L.) Kuntze. The last two are the most common of the vines found in this habitat.

Herbaceous vegetation is at a minimum. *Hydrocotyle* spp., and *Centella repanda* (Pers.) Small seem to be the most common over the ground of these hammocks as a whole. Occasionally one finds

small patches of *Mariscus jamaicensis* (Crantz.) Britton, *Spartina bakeri* Merr., *Osmunda regalis* L., and *Thelypteris thelypteris* (L.) Nieuwl.

The top layer of soil is composed of black organic muck which is held together by a heavy network of small roots, etc. On top of this is a comparatively thick layer of leaves. The lower part of this leaf cover is wet, but the top layers may be dry during the winter. The soil is built up around the bases of the trees to form hummocks of drier soil. These are sometimes very wide about the tree bases and may connect with those nearbly. Numerous large, rotten logs are scattered over the ground. Most of them are always very wet.

Fifteen species comprise the orthopteran assemblage of the habitat. They are distributed among three distinct strata; (1) the terrestrial stratum, which is made up of two ecological niches, (1a) the bare, medium-wet soil and (1b) the leaf duff and decaying wood on the floor of the hammock; (2) the shrub stratum, and (3) the broad-leaved arboreal stratum.

Dominant: *Tetrix arenosus arenosus* (Burmeister) 3-A, *s1a* s1b; *Neotettix bolteri* Hancock 4-A, *s1a* s1b; *Tettigidea lateralis lateralis* (Say) 4-A, *s1a* s1b; *Nemobius carolinus carolinus* Scudder 4-C, s1a *s1b; Anaxipha exigua* (Say) 4-A, s2; *Hapithus agitator quadratus* Scudder 4-A, s2.

Frequent: None.

Occasional: *Vostox brunneipennis* (Serville) 2-A, s1b; *Cariblatta lutea lutea* (Saussure & Zehntner) 2-F, s1b; *Tettigidea armata* Morse 2-A, *s1a* s1b; *Romalea microptera* (Beauvois) 2-F, s1b.

Infrequent: *Prolabia pulchella* (Serville) 1-A, s1b; *Parcoblatta fulvescens* (Saussure & Zehntner) 1-F, s1b; *Nomotettix cristatus floridanus* Hancock 1-N, *s1a* s1b; *Pterophylla camellifolia camellifolia* (Fabricius) 1-F, s3; *Lea floridensis* (Beutenmuller) 1-F, s2 *s3*.

The Alluvial Hammock Habitat assemblage of Orthoptera is most closely similar to that of the Low Hammock Habitat, as was pointed out in the discussion of the latter and where also the major differences between the two were mentioned. All of the species found in the alluvial hammocks were taken also in the low hammocks with the exception of *Anaxipha exigua*, which occurs in the thickets of small ash (*Fraxinus pauciflora*) along the river's edge, and the possible exception of *Pterophylla c. camellifolia*. The percentage composition of the different species in the assemblages of these two habitats is, however, quite different, and from this standpoint they have been separated.

Edificarian and Miscellaneous Habitats

The following habitats cannot be considered equivalent to those which have thus far been discussed. They are not based on correlations with vegetation (except the Water Hyacinth Habitat, and to some degree, the Shell Mound Habitat), soil, water relations, etc., but are a group of environments which do not fit well into the classification of the more natural and extensive ecological units already described.

Edificarian Habitat

The following species were found in the various buildings on the reserve: *Supella supellectilium* (Serville) 1-A; *Blattella germanica* (L.) 1-A; *Periplaneta americana* (L.) 4-A; *Periplaneta brunnea* Burmeister 4-A; *Periplaneta australasiae* (Fabricius) 2-A; *Cycloptilum trigonipalpum* (Rehn & Hebard) 1-F.

The building in the present quail hatchery enclosure, in which grain and other feed is stored, and the dormitory building, where food is kept, support the largest populations of roaches, mainly *Periplaneta americana* and *Periplaneta brunnea*. *Supella supellectilium* and *Blattella germanica* were very infrequently found, but they were locally abundant at times. Several *Cycloptilum trigonipalpum* were collected in the dormitory building, but they are to be considered erratic individuals. In addition to the above list, numerous species were found in the laboratory and dormitory buildings, having been trapped inside after being attracted to the lights at night. Notable among these were the males of *Parcoblatta fulvescens* (Saussure & Zehntner) and *Nemobius fasciatus socius* Scudder.

Wood Pile Habitat

Before the reserve came under the jurisdiction of the University of Florida, a large part of the fallen timber (mostly pines) was gathered and sawed into short lengths to be stacked just east of the present mess-hall. Other smaller wood piles were kept behind the forester's house, the fire towerman's house, and at the quail hatchery. Under the bark of the short logs in these piles, and beneath the logs and boards lying on the ground, the following species were collected: *Prolabia pulchella* (Serville), *Parcoblatta fulvescens* (Saussure & Zehntner), and *Eurycotis floridana* (F. Walker). *Doru lineare* (Eschscholtz) was found in the wood pile near the mess-hall. Individuals of this species migrated to the wood pile from the nearby heavy growth of the land ecotype of *Panicum hemitomon* after the stalks of this plant had died in the late fall.

Shell Mound Habitat

Most of the shell mound at the tip of Orange Point has been excavated so deeply that in spots large puddles of water stand in the pockets thus formed. Plants have quickly become established over much of the recent excavations and especially around and in these small pools. A small amount of organic matter has been deposited in these places and is mixed with the shells, making them less firmly consolidated than on the higher parts of the mound where they are more or less cemented together. The areas about the puddles seem to be ideal for *Scapteriscus acletus* Rehn & Hebard and *Tridactylus minutus* Scudder which are very abundant here. Over the entire excavations, on the higher drier portions, as well as around the puddles, *Paratettix cucullatus cucullatus*

(Burmeister) and *Paratettix rugosus* (Scudder) abound.

WATER HYACINTH HABITAT

Water hyacinths grow in great profusion in the St. Johns River. Winds, tides, and currents constantly move large floating mats of these plants up and down the river and back and forth from bank to bank. In the small coves and places where they are protected from these moving agents, the hyacinths accumulate in very large masses, sometimes one hundred yards or more in width. On these mats the following species have been found: *Romalea microptera* (Beauvois) 1-N, *Orchelimum pulchellum* Davis 4-A, and *Anaxipha pulicaria* (Burmeister) 2-C.

The mats form near shore, whence they obtain their orthopteran inhabitants. Since large sections break away from the main mass at various times and are carried from place to place, these moving bodies of water hyacinths constitute a very potent means for the dispersal of the forms mentioned and doubtless many other species which wander onto them. While in a boat in the middle of the river, I have often heard individuals of *Orchelimum pulchellum* and *Anaxipha pulicaria* vigorously singing as they floated by on their rafts.

SYNOPSIS OF THE ORTHOPTERAN HABITATS OF THE WELAKA AREA

Xeric Associations:
- Sparsely-Vegetated Land and Herbaceous vegetation
  1. Dry, Sparsely-Vegetated Sand Habitat
  2. Lawn Habitat
  3. Dry, Ruderal Grassland Habitat
     - a. Hypogeic stratum. Common to 1, 2, and 3
     - b. Bare, terrestrial stratum. Common to 1, 2, and 3
     - c. Herbaceous and shrub stratum. Common to 2 and 3
     - d. Coniferous arboreal stratum. Poorly represented in 2
- Non-Hammock Vegetation
  4. Scrub Habitat (*Pinus clausa*-dwarf oak and *Pinus australis*-dwarf oak vegetational associations)
  5. Sandhills Habitat (*Pinus australis-Quercus laevis* vegetational association)

     Strata more or less common to these habitats are:
     - a. Hypogeic stratum
     - b. Terrestrial stratum
     - c. Herbaceous and shrub stratum
     - d. Coniferous arboreal stratum
- Hammock Vegetation
  6. Xeric Hammock Habitat (*Quercus virginiana* vegetational association)
     - a. Hypogeic stratum
     - b. Terrestrial stratum
     - c. Herbaceous and low shrub stratum
     - d. Tall shrub stratum
     - e. Coniferous and broad-leaved arboreal stratum

Mesic Association:
- Hammock Vegetation
  7. Mesic Hammock Habitat (*Magnolia-Ilex* vegetational association)
     - a. Hypogeic stratum
     - b. Terrestrial stratum
     - c. Herbaceous and shrub stratum
     - d. Broad-leaved arboreal stratum

Poorly Drained and Meso-Hydric Associations:
- Sparsely-Vegetated Land and Herbacous Vegetation
  8. Moist, Sparsely-Vegetated Sand Habitat
  9. Moist, Ruderal Grassland Habitat
  10. Pond Margin Habitat

      Strata more or less common to these habitats are:
      - a. Hypogeic stratum
      - b. Terrestrial stratum
      - c. Mixed herbaceous and scant shrub stratum
- Shrub-Dominated Vegetation
  11. Marginal Thicket Habitat (*Pinus palustris-Aronia-Serenoa* vegetational association)
      - a. Hypogeic stratum
      - b. Terrestrial stratum
      - c. Shrub stratum
- Flatwoods Vegetation
  12. Longleaf Pine Flatwoods Habitat (*Pinus australia-Aristida stricta* vegetational association)
  13. Shrubby, Longleaf pine Flatwoods Habitat (*Pinus australis - Serenoa - Desmothamnus-Xolisma-Cyanococcus* vegetational association)
  14. Black Pine Flatwoods Habitat (*Pinus serotina-Desmothamnus* vegetational association)
  15. Slash Pine Flatwoods Habitat (*Pinus palustris-Aristida-Andropogon* vegetational association)

      Strata more or less common to these habitats are:
      - a. Hypogeic-terrestrial stratum
      - b. Herbaceous and shrub stratum
      - c. Coniferous arboreal stratum

Hydric Associations:
- Herbaceous Vegetation
  16. Pond Habitat (*Panicum hemitomon-Castalia-Utricularia* vegetational association)
  17. Spartina Marsh Habitat (*Spartina bakeri* vegetational association)
  18. Saw grass Marsh Habitat (*Mariscus jamaicensis* vegetational association)

      Strata more or less common to 17 and 18 are:
      - a. Wet terrestrial stratum
      - b. Emergent herbaceous stratum
      - c. Shrub stratum

Tree-Dominated Vegetation

19. Bayhead Habitat (*Gordonia-Magnolia-Tamala* vegetational association)
20. Low Hammock Habitat (*Liquidambar-Tamala-Ulmus-Sabal* vegetational association)
21. Alluvial Hammock Habitat (*Taxodium-Nyssa-Fraxinus-Rufacer-Sabal* vegetational association)

Strata more or less common to these habitats are:

a. Hypogeic stratum
b. Terrestrial stratum
c. Shrub stratum
d. Broad-leaved arboreal stratum

Edificarian and Miscellaneous Habitats:

22. Edificarian Habitat
23. Wood Pile Habitat
24. Shell Mound Habitat
25. Water Hyacinth Habitat

Graphic Analysis of the Orthopteran Habitats and Species Assemblages

Figures 16a, b, and c present a graphic analysis of the orthopteran habitats, their species assemblages, and the quantitative analysis of these associations. The twenty-two vertical columns are headed by the recognized major habitats of the Welaka area. The arrangement of these on the charts does not conform to the arrangement as given just previously in the tabular synopsis. Instead, on the charts, an attempt has been made to place those habitats close together whose species assemblages are most nearly alike as far as species go, although the percentage composition may be different. It is obvious that, since no two habitats are exactly alike either in species or percentage composition, a perfect arrangement to fit all cases is impossible. It appears that the arrangement given on the charts is the most satisfactory one from the standpoint of showing the "blocks" of habitats which the species occupy. The species have been arranged vertically in standard taxonomic sequence.

The blank squares indicate that the species was not found in the habitat. In those habitats where a species was found the abundance and frequency of the species in that situation is shown by two rectangles, side by side. The black rectangle on the left side indicates the relative abundance. The maximum length of the column represents the classification "abundant" as previously defined on page 93; three-quarters length represents "common"; one-half length represents "numerous"; and one-quarter length represents "few." It must be emphasized here that any one of the above classifications, viz., abundant, common, etc., is not numerically equivalent for all species. As explained before, abundant does not mean that 100 or 200 or any definite number of individuals could be collected in a specified length of time, regardless of the species concerned. Rather, the term abundant, as well as the other categories,

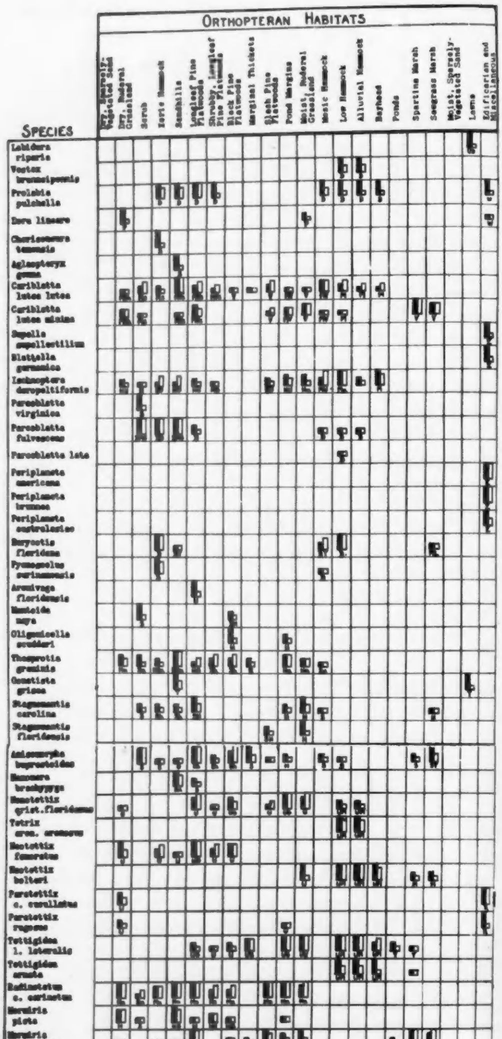


FIG. 16a. For an explanation of this figure, refer to the preceding paragraphs under Graphic Analysis of the Orthopteran Habitats and Species Assemblages. A key to the letter symbols in each rectangle of abundance and frequency is as follows: A, broad-leaved arboreal stratum; B, in burrows of other animals; C, coniferous arboreal stratum; D, on or in decaying wood; E, edificarian; G, on low mat grasses; H, on herbage; L, in saw grass leaf sheaths; M, in or under decaying leaves on the ground; O, in self-constructed burrows; P, on a specific plant; R, shell mound habitat; S, on shrubbery; T, on tree trunks; U, on bare, dry to medium wet soil; V, under vegetation; W, under pieces of wood or logs (not necessarily decayed); X, attracted to electric lights; Y, on emergent aquatic vegetation; Z, on water hyacinths.

is an estimate of the numerical status of that particular species in a particular situation with respect to the other situations in which it may be found at the time of maximum abundance of the species in the entire Welaka area. Numerical comparisons between species are, therefore, not possible; the only valid comparisons which can be made are between the different habitat occurrences of a single species. The white rectangle on the right indicates the relative frequency with which the species occurs in the habitat. The maximum length of the rectangle indicates a frequency of 100% or the symbol 4 as indicated on page 93; three-quarters length represents a frequency averaging approximately 75% or the symbol 3; one-half length equals a frequency averaging approximately 50% or the symbol 2; and one-quarter length represents a frequency averaging 25% or less, or the symbol 1.

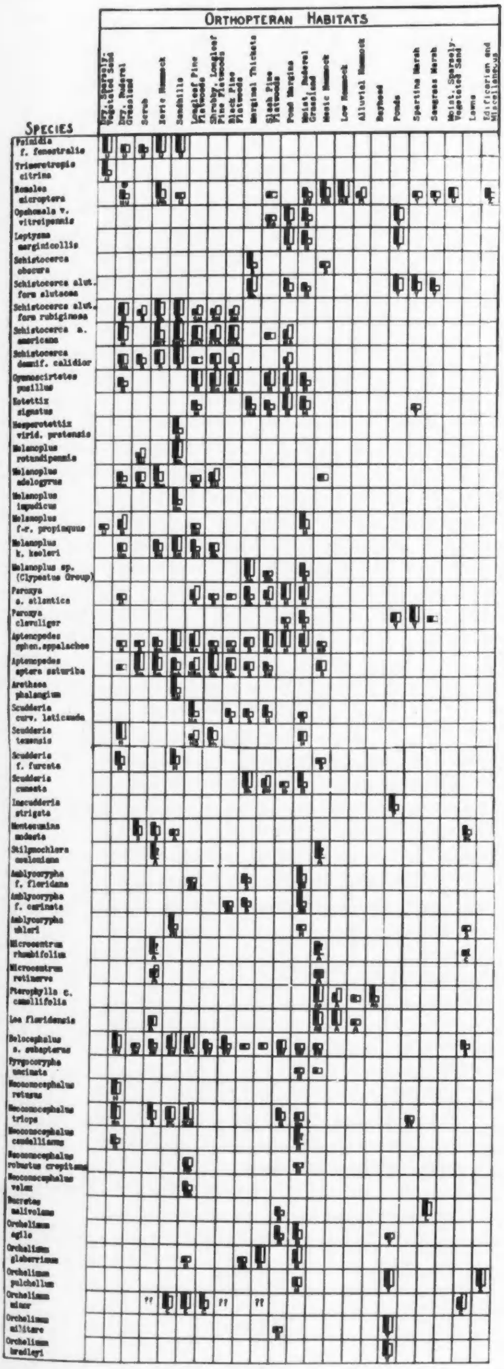


FIG. 16b. CONTINUATION of FIG. 16a.

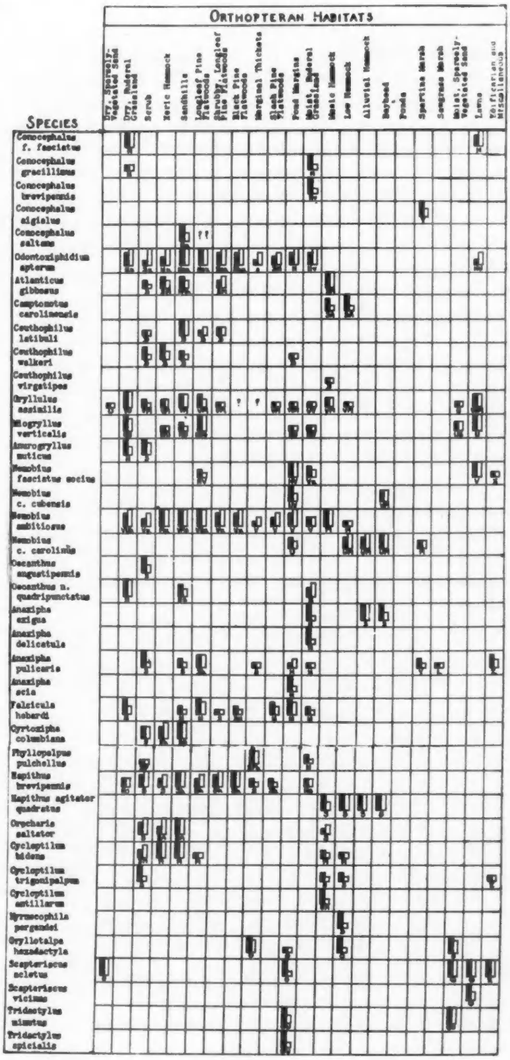


FIG. 16c. CONTINUATION of FIG. 16a and 16b.

In those cases where the data are insufficient to establish the presence of the species in a habitat, but where it is believed they occur in relatively few numbers, their presumed presence is indicated by a dotted outline of the abundance-frequency rectangles, and the abundance rectangle is shown by diagonal lines rather than being solid black.

Symbols beneath the rectangles of abundance and frequency indicate the minor habitat or ecological niche which each species occupies within the major habitats. Capital letters indicate the primary ecological niche in which the species is generally found. Symbol letters in lower case indicate a secondary ecological niche in which the species may also be found.

SUCCESSION

Laessle (1942) has given a very lucid and thorough presentation of the plant succession as it occurs in the Welaka area. His conclusions, based upon painstaking investigation and clear analysis, are that the plant associations have developed in response to the soil types and their evolution, water relations, and topography, with fires playing a very important role in succession. A diagrammatic chart of the successional stages has been presented there, and this formed the basis for a similar, modified diagram showing the relation of the orthopteran habitats to the phytoecological habitats and successional stages.

It has been emphasized that the orthopteran associations are closely correlated with the vegetation and that this fact was used as a basis for the habitat classification of the former. The physical factors of soil, water relations, and topography are of importance in the evolution of the plant associations as well as the orthopteran assemblages. Vestal (1913) showed this close relationship of the Orthoptera to the vegetational aspects for the Douglas Lake region in Michigan and worked out a detailed diagram of the successional stages in the vegetation and the correlated insect associations. The picture of the plant succession for the Welaka area, as presented by Laessle, afforded an opportunity to correlate the succession of the orthopteran assemblages in these plant habitats. Since a considerable number of orthopteran habitats were not recognized as separate plant associations, it was necessary to modify Laessle's successional diagram to fit these cases. These relations are presented in Fig. 17. In addition to some explanations given in this figure, further explanations of the successional stages have been presented in the descriptions of the orthopteran habitats.

SUMMARY

After an introductory discussion of previous studies on the ecology of the Orthoptera, the two main objectives of the present investigation are stated: (1) to determine what species of Dermaptera and Orthoptera occur in the Welaka area, Florida, and (2) to work out a classification of the habitats of the area, based upon the occurrence and ecological relations of the insects themselves. Important literature relating to this region and to the specific problem is briefly mentioned.

The Welaka area, and more particularly the University of Florida Conservation Reserve, is described as to its location, history, and zonal relations of the biota, its climate, geology, and soils. The descriptions are sufficiently detailed to enable ecologists to compare this area with others that have been or may in the future be investigated along similar lines. Climatic charts and graphs, a generalized map of the Pleistocene shore lines near Welaka, and a detailed soil map of the reserve are included. This material furnishes the background and part of the data for the detailed descriptions of the vegetational associations that constitute the orthopteran habitats, and helps to explain the presence or absence and the local distribution of some of the species. In the instance of certain brachypterous species, which, though common in peninsular Florida proper, fail to reach Welaka and the area east of the St. Johns River, such as *Melanoplus puer puer* and *Macneillia obscura*, and in the converse case of similar species which are confined to the Welaka region, such as

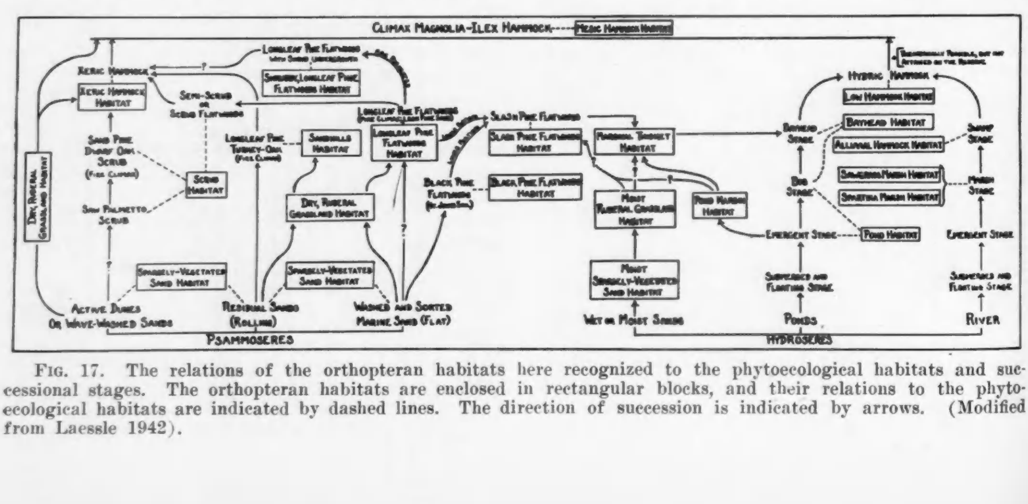


FIG. 17. The relations of the orthopteran habitats here recognized to the phytoecological habitats and successional stages. The orthopteran habitats are enclosed in rectangular blocks, and their relations to the phytoecological habitats are indicated by dashed lines. The direction of succession is indicated by arrows. (Modified from Laessle 1942).

Melanoplus adelogyrus and *Aptenopedes aptera saturiba*, Hubbell's hypothesis (1932) of insular isolation of the area is additionally supported, although present knowledge indicates that the isolation must be attributed to Pleistocene and not earlier submergence. It is to be noted that the species showing such a relation to the St. Johns River barrier are all species of relatively dry environments, those inhabiting moist or wet situations having not found the river and its bordering swamps and marshes an insurmountable barrier.

At this point are outlined the organization of the field work and the methods used in the recording and analysis of the field data. The difficulties encountered in field determinations of frequency and abundance of orthopteran species are noted, and a summary is given of the methods that others have proposed for making such determinations together with the methods used in the course of this study.

Twenty-five orthopteran habitats are recognized as occurring in the Welaka area. Following a general critique of the types of classifications proposed by previous workers, the basis for the classification here followed is presented. None of the ecological classifications of orthopteran species proposed to date is wholly satisfactory nor applicable to the whole group because of the following factors: the wide variety of habits shown by the different species and species groups; response to different features of the environment; difference in habitat distribution between the immatures and adults, during the day and at night, and from one part of the annual season to the next; differences in behavior of the same species in different parts of its range. In this present study the classification is based upon the principal plant associations, with recognition given to the influence of soil, water, and topographic relations. The concept of major and minor habitats was found necessary in order adequately to define the habitat relations of the orthopteran species. The actual selection of the recognizable habitats was made after analysis of the data obtained by collecting some 10,000 adults and 14,000 juveniles in all parts of the area. In addition, many thousands of other individuals were observed in the field and records made of their occurrence, abundance, frequency, and activities. Collecting was carried on over a period of fifteen months, during which time almost daily field work was done. The twenty-five habitats finally recognized include sixteen natural associations, five ruderal associations, and four very special types of situations.

The dermapteran and orthopteran assemblages of the habitats were studied and analyzed with respect to the following points:

(1) Quantitative composition. After a critique of the methods already used by various authors for determining and describing this composition, a modification of that proposed by Vestal (1913), Rogers (1942), and Cantrall (1943) was adopted for the present study. Four categories of occurrence in a habitat are recognized, and these are Dominant, Frequent, Occasional, and Infrequent. It is concluded that the most nearly satisfactory method of determining the relative abundance of a species in a given habitat is that of estimate by an experienced collector thoroughly familiar with the species, after repeated collecting carried on at all seasons of the year and times of day, and by a variety of methods. Other proposed methods, at first sight more objective, all prove in practice to be open to serious criticism.

(2) Habitat distribution and type of occurrence within a habitat. The relations of the species to the habitats in which they occur are described, giving the dominant plants of the vegetational strata, and discussing the soil, water relations, role of fire, presence or absence of leaf duff, and in some instances the successional relations, as influencing the orthopteran inhabitants. The orthopteran species of each habitat are listed, with an indication of their abundance, frequency, and relations to minor habitats or strata. The twenty-five orthopteran habitats present on the reserve differ from one another, not merely in the presence or absence of particular species, but more especially in the presence in each of numerous species also found in other habitats, but occurring in a distinctive frequency-abundance pattern characteristic of each individual habitat. A tabular synopsis and graphic analysis are given of the dermapteran and orthopteran habitats and their species assemblages. The habitat distribution charts illustrate the fact that the species in general fall into two groups; those that occur more or less throughout the major habitat, making use of different parts of it at different times of the day or in different stages of development, and seemingly influenced chiefly by the broad general features of the situation, such as the amount of exposed soil and quantity of vegetation; and on the other hand those species that are definitely associated with some minor habitat, such as a vegetational stratum, a specific food plant, or a particular soil condition. The charts illustrate the role of the minor habitat in enabling certain species to live in major habitats that differ widely in humidity, soil conditions, water relations, etc. These charts also emphasize the manner in which taxonomic groupings of species, such as the Oedipodinae and Tetiginae, assert their common genetic background in their similar ecological responses, and in occupying a definite sector of the humidity scale.

(3) Succession. Orthopteran succession follows and is dependent upon plant succession. It proved impossible to make such a successional diagram as that presented by Vestal (1913) for the Acrididae of the Douglas Lake region of Michigan, but the essential data for such orthopteran succession as could be recognized are contained in the habitat descriptions and are presented graphically (Fig. 17) in relation to recognized phytoecological habitats and stages of plant succession.

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THE PAST AND PRESENT VEGETATION OF HIGH POINT STATE PARK, NEW JERSEY

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INTRODUCTION

The objective of this paper is to describe and correlate the past and present vegetational patterns and point out future successional trends in the plant communities of High Point State Park. The descriptions of vegetation are intended to be suitable for general use as well as to contribute to the vegetational knowledge of northwestern New Jersey. High Point State Park was selected for the study since no detailed investigations had been made in the region. Furthermore, it represented a delimited area which was relatively free from disturbance since its acquisition as a State Park.

The park is located in Sussex County in northwestern New Jersey. It is an area of 10,935 acres lying just south of the New York State line and saddling the crest of the rocky Kittatinny Mountains for a distance of 8 mi. (Fig. 1). Its southern boundary is contiguous with Stokes State Forest. In width it ranges from 2 to 4 mi. depending upon various irregularities of the boundary. The area has not long been a State Park. It was given to the State of New Jersey by the late Colonel and Mrs. Anthony Kuser in 1923. They had built a 220 ft. monument at the highest point on the ridge which is also the highest elevation in New Jersey (Fig. 1). The monument affords an excellent perspective of the park. During the peak of autumn coloration the differential aspect of the various communities is pronounced. Light green pitch pine characterizes the rock outcrops of the ridge top, with a colorful oak forest predominating on the slopes. Dark green conifers are conspicuous in the bogs and swampy areas surrounding the lakes (Fig. 2).

The high series of ridges in the park owe their presence to the geological structure of the region. Physiographically, this part of the State lies in the Ridge-Valley Province. The rocks are of Paleozoic age. The limestones, shales, sandstones, and conglomerates were subjected to normal and thrust faulting as well as complex folding during the latter part of the Paleozoic. In Tertiary time, the land was base leveled forming the Schooley peneplain (Kummel 1940). With the uplift of the Schooley peneplain in late Tertiary time, the streams were rejuvenated. The harder strata of sandstone and conglomerate resisted rapid erosion and today persist as ridges while the less resistant shales and limestones form adjacent valleys. East of the Kittatinny ridge, shales and limestones underlie the Kittatinny valley. The ridge is double crested, the eastern part forming the major ridge (Fig. 2, 3). It consists of Shawangunk conglomerate which is primarily quartzitic with small white quartz and slate pebbles embedded in a siliceous matrix. To the east the ridge drops off as a steep, and in places, precipitous escarpment. Toward its base the Martinsburg shale outcrops, its beds dipping northwest under the conglomerate (Salisbury 1902).

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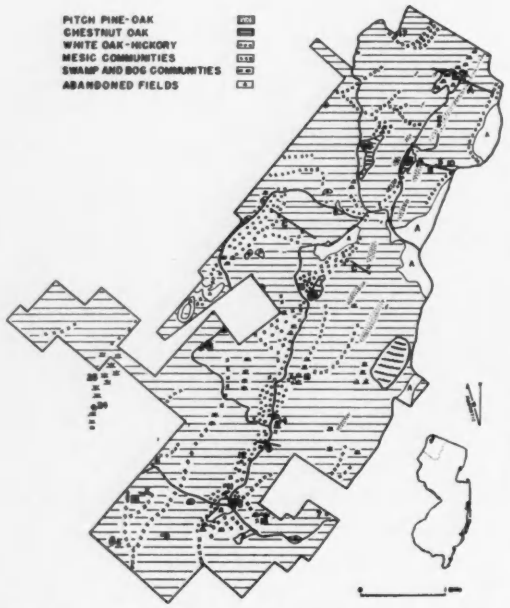

FIG. 1. Vegetational map of High Point State Park. Locations of stands (1-19) studied in detail are designated by solid dot adjacent to the number. Other areas studied in less detail are designated by numbers 20-25. Transects A, B, C, D, E, are indicated by solid lines. Stippled areas in eastern sector of park represent pitch pine-scrub oak community on the conglomerate ridge top. In general these areas correspond to the high rocky outcrops. In most cases, the streams can be located from the pattern of the mesic communities. The mesic communities include the mixed oak-hardwoods and northern hardwoods. Lakes are indicated by wavy lines (20-24). In the east central sector of the park is the Sussex reservoir (Lake Rutherford). Heavy irregular lines indicate roads. High Point Monument is located at the terminus of the road south of stand 2. Lower right outline map of New Jersey with Sussex County and park located.

However, on the ridge top near the park entrance a small lobe of shale extends northward to Lake Marcia. The lower western ridge crest is developed upon the High Falls formation consisting of red, green, and olive-colored sandstone and shale with interspersed beds of conglomerate. The topography is less rugged than where the Shawangunk occurs. Maximum elevations on the two geological formations are strikingly different. The Shawangunk ridge where the High Point Monument is located rises 1803 ft. above mean sea level (Fig. 1). In contrast the highest ridge on the High Falls is only 1480 ft.

During the Pleistocene epoch, the area was glaciated. At least two and possibly three ice sheets advanced southward covering the northern part of the State (Kummel 1940). Each modified the topography by both scouring the highest ridges and elsewhere leaving in its retreat extensive glacial deposits. The pronounced glacial features of the area are due to the most recent glaciation, the Wisconsin—specifically the Cary substage, the final Mankato advance terminating further north (P. MacClintock, personal communication). The terminal moraines of the Wisconsin extend as far south as a line extending across the State through Perth Amboy, Morristown, Hackettstown and Belvidere. Glacial striae on the scoured conglomerate outcrops indicate that the ice sheet moved across the area of the park in a southwesterly direction. The topography influenced the distribution of the glacial drift. It is estimated to reach 10 ft. or more in depth on the High Falls while along the crest of the Shawangunk ridge it does not exceed 2-3 ft. (Salisbury 1902). Over the latter it is sporadic and interspersed with rock outcrops. The steeper slopes are talus covered as a result of either glacial plucking or the disrupting action of temperature changes in post-glacial time. Glacial lakes formed either by dammed up valleys or scoured out basins characterize the area.

For the most part the soils have been derived from the weathering of glacial drift. On the drift overlying the High Falls the soil has been mapped as the Lackawanna stony loam (Jennings, *et al* 1903). In the depressions on the major ridge, a shallow phase of this type may be recognized. The profile developed is either a true podzol or of the gray-brown podzolic type. The latter is most widespread. It is a brown to reddish-brown loam 5-8 in. deep grading into a yellow-brown to Indian red subsoil. The parent material exposed at a depth of about 2 ft. along the road cut is bouldery clay. It consists of a mottled dark-brown to light-gray matrix containing many boulders and rock fragments.

On the Shawangunk formation rock outcrops are common. Here where soil has formed at all it is by the slow process of the accumulation of organic material and weathering of the parent materials.

The park has an annual mean temperature of 49.5°F. (Sussex, 22-yr. record) with extremes ranging from −20° to +100°F. The frost free season extends from May 7th to October 1st (Culvers Lake). The annual mean rainfall is 45.94 in. (Culvers Lake) with most of it occurring during the summer. Much of the precipitation in winter is in the form of snow with occasional sleet and ice storms. The annual snow cover is 54.5 in. (Culvers Lake) or 10% of the total precipitation. Snow to a depth of 20 in. in one storm is not unusual. The wind direction is southwest during July and August but from the northwest during the rest of the year (U. S. Dept. Agr. 1926).

The park lies in the oak-chestnut forest region which extends southward along the Ridge-Valley and Blue Ridge Provinces (Blodgett 1910; Braun 1950). To the east on the Piedmont of North Carolina, this forest gives way to oak-hickory (Oosting 1942) which also occurs northward on the Piedmont of New Jersey (Bard 1952). To the north and northwest on the Allegheny Plateau, chestnut-oak is replaced by the hemlock-white pine-northern hardwoods as described by Nichols and others (Nichols 1913a, 1935; Lutz 1928, 1930; Bray 1930; Hotchkiss 1932; Hough

Fig. 2. View north from top of High Point Monument in autumn. On ridge at right, pitch pine-scrub oak community demarked by green areas of pitch pine. Contiguous with it is chestnut oak community represented by orange-yellow coloration. This community also predominates on the adjacent slopes. In center at base of slope, Cedar Bog with dark green coniferous element (hemlock, black spruce, southern white cedar) and interspersed reddish-yellow deciduous element (red maple, yellow birch, black gum). Reddish tinge, at base of slope and especially beyond the bog, indicates the presence of other oak species. Grayish-white areas on ridge top within pitch pine-scrub oak community are conglomerate rock outcrops surrounded by scarlet colored ericaceous shrubs. Dark areas beyond bog are cloud shadows. (This illustration published with funds other than those of Ecological Monographs.)

FIG. 3. View south from top of High Point Monument. Shawangunk conglomerate forms major ridge which continues southwestward. Less rugged topography of High Falls formation to right of major ridge. Pitch pine-scrub oak community in foreground left of road (Stand 1). Note burned-over area left of center, indicated by carpet-like area of low shrub vegetation. Lake Marcia at right. Fields are on Martinsburg shale at left. Lake Rutherford and Saw Mill Pond in left and right background respectively.

1936; Gordon 1940; Egler 1940; Hough & Forbes 1943). Bray (1930) studying the vegetation of New York State, points out that the State lies in a transition zone where oak, chestnut, and hickory overlap with the northern hardwoods, the birch, beech, hemlock, and sugar maple. Similar patterns in more detail have been observed by Raup (1938) in the rugged Black Rock Forest of New York and by Jennings (1939) in the mountainous Ridge-Valley Province of Pennsylvania. Within the High Point region, as early as 1884, Britton noted a striking similarity between the pitch pine-scrub oak on the Kittatinny ridge and the Pine Barrens of southern New Jersey. He also observed the presence of a peculiar flora characteristic in part of more northern regions, or in part, the coastal plain of New Jersey. Around 1900 the geological and soil surveys reported a mixed coniferous deciduous forest (Vermeule, *et al* 1900). Jennings and his co-workers found a forest predominantly of oak-chestnut (Jennings, *et al* 1913). Moore (1939) reports a forest primarily of mixed hardwoods in which oak is dominant. Recent comparative studies on the life forms in the pine-oak community compared with those in the Pine Barrens of New Jersey, indicate a greater proportion of hemicryptophytes and cryptophytes on the ridge than in the Pine Barrens, which is suggestive of the more rigorous climate of the ridge (Archard 1953, in press).

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METHODS

The field work was conducted during the summers of 1950 and 1951. A systematic reconnaissance of the park was undertaken by following a series of compass lines selected on the basis of a study of aerial photographs and topographic maps. Then long transects were established through sections of the park, cutting across successive communities. Along these transects tree cover was measured by the line intercept method (Bauer 1943, Buell & Cantlon 1950). This served to show the relationship of the communities to the topography and to each other. There were five such transects (A, B, C, D, E). Next, individual stands were sampled (Stands 1-19). Locations of transects and stands are shown in Fig. 1. Again the line intercept method was used to determine cover in both the tree and shrub layers. In each community a line of 100 m. was used except where only a single stand of a type was sampled. In the latter case, the size of the sample was increased depending upon the uniformity of the community. For instance, in the mixed oak-hardwoods community a transect of only 160 m. was used. Diameters of all trees which occurred in a continuous 4 m. strip along the transect line were measured. Saplings (including individuals of tree species 1 ft. high or over but less than 1 in. d.b.h.) were counted on a continuous 2 m. strip along the transect line. Herb and moss cover was estimated on $\frac{1}{2}$ x 2 m. quadrats spaced at 5 m. intervals along the transect line. Tree seedlings were counted in the $\frac{1}{2}$ x 2 m. quadrats.

Specimens of all species found were collected and

have been deposited in the Chrysler Herbarium of Rutgers University. Nomenclature for the vascular plants is according to Gray's Manual (8th ed. Fernald 1950); mosses according to Grout (1940).

Soil samples were taken in the communities studied. The pH of the samples was determined with the Beckman pH meter after the soil had been brought into the laboratory. The dry soils were soaked 24 hours before testing using a soil-water ratio of 1:2.5.

Peat samples for pollen analysis were obtained from Cedar and Pine bogs. The samples were taken at 1 ft. intervals with the Davis-type peat sampler. In the laboratory the pollen was separated by the KOH method (Sears 1930). Counts of 150 grains were made except in the lower clay layers where, because of a paucity of pollen, a minimum of 50 grains was counted. Such low pollen samples come from the 33 to 38 and 40 ft. levels of Pine Bog and the 20 ft. level in Cedar Bog. Percentages are based on total tree pollen.

RESULTS

XERARCH SUCCESSION

The earlier stages of primary succession are characterized by the covering of exposed rock surfaces with vegetation and its accompanying soil accumulation. The pioneer invaders on the bare rocks are usually crustose and foliose lichens. The formation of moss-lichen mats occurs in the depressions or from the periphery of the rock outcrops. As soil accumulates within these mats, grasses and sedges are able to become established. With further accumulation ericaceous shrubs and trees of the surrounding forest invade and eventually cover the exposed rock surfaces. This succession is well shown on the exposed outcrops of the ridge top, contiguous with the pitch pine-scrub oak community (Fig. 2). Growing on the dry exposed rock surfaces of the ridge top, crustose lichens must withstand extreme periods of drought. Most conspicuous of them is *Rinodina oreina* (Ach.) Mass. which grows so closely appressed to the rock that it appears to be a part of it and gives the conglomerate a blackish-gray appearance (Fig. 4). Foliose forms such as *Crocynia neglecta* (Ach.) Hue. and *Parmelia conspersa* (Ehrh.) Ach. var. *isidata* (Anzi.) Stizenb. also grow on the bare rock surfaces where they frequently cover and destroy the crustose forms. Crocynia appears as irregular gray patches and Parmelia forms circular greenish gray patches. In addition two members of the Umbilicariaceae, *Actinogyra muhlenbergii* (Ach.) Schol. and *Lasallia pensylvanica* (Hoffm.) Llano form black scaly masses on the rock surfaces. These lichens do not develop mats upon which higher plants can grow. The soil building pioneers which start in the crevices and depressions or from the periphery of the outcrops here, as in North Carolina (Oosting & Anderson 1937), do not appear dependent upon the presence of crustose lichens. *Bryum capillare* and *Ceratodon purpureus* are the earliest forms to appear in the crevices. They are particularly important on the ledge near the monument where they occur with *Potentilla tridentata* (Fig. 4). These three, Bryum, Ceratodon, and Potentilla also occur in an admixture of soil and conglomerate fragments surrounding the outcrops. Other mosses which commonly form tufts and mats in the crevices or depressions are *Polytrichum juniperinum, P. commune, Leucobryum glaucum, Dicranum scoparium* and *D. fulvum*. *Cladonia*, especially *C. caroliniana* (Schwein.) Tuck. may occur with any one or combinations of these species and eventually form expanding mats which spread out over the rock surface. Similar mats form from the edge and advance out over the rock. The thickness of the moss-lichen mats increases as the lower portions of the mosses and lichens die and add humus to the organic layer and as dust and dirt sift down into them.

FIG. 4. Xerarch succession on Shawangunk conglomerate at High Point Monument. *Rinodina oreina* gives conglomerate gray tone. Umbilicariaceae form black scaly patches at right. In crevices *Potentilla tridentata* is flowering. Note *Pyrus melanocarpa* at left.

With the increase in thickness of the mat, growing conditions improve, especially moisture holding capacity, and herbs can grow on the mat. *Deschampsia flexuosa* is among the first and along with it may be *Danthonia spicata, Panicum depauperatum, Andropogon scoparius*, and *Carex pensylvanica*. In crevices on the more exposed sites, Carex, Danthonia and Panicum frequently occur with the mosses and lichens. During this open herbaceous stage pine seedlings become established. Finally, with further growth of the mats, low shrubs invade either on the periphery or in the center of the mat. In order of decreasing importance on the mats they are *Vaccinium angustifolium, Gaylussacia baccata, Pyrus melanocarpa, Vaccinium vacillans, Kalmia angustifolia, Amelanchier stolonifera* and *Vaccinium stamineum*. Where soil accumulates in the deeper fissures of the bed rock, shrubs may invade directly. Here Pyrus or one or more of the above shrubs is frequently found. Scrub oak (*Quercus ilicifolia*) becomes established on the mat only after it has reached considerable thickness. Herbaceous cover beneath the shrubs is similar to that found in the pitch pine-scrub oak community.

In contrast to the exposed ridge top is the north-

FIG. 5. Northwest facing talus slope above Cedar Bog. Note sweet birch and white birch. Rhododendron is dominant shrub.

west talus slope (Fig. 5). There much of the slope is partially shaded by chestnut oak (*Quercus prinus*), sweet birch (*Betula lenta*), white birch (*Betula papyrifera*), white pine (*Pinus strobus*), striped maple (*Acer pensylvanicum*), mountain maple (*Acer spicatum*) and mountain ash (*Pyrus americana*). Such slopes are strewn with large conglomerate boulders on which the earlier lichen stages are similar to those on the ridge except for an abundance of Umbilicariaceae. Among these *Lasallia papulosa* (Ach.) Llano is dominant, forming large grayish-black scale-like growths. In addition *Umbilicaria mammulata* (Ach.) Llano and *Actinogyra muhlenbergii* are present. Where the boulders are shaded, these species increase in cover so that little of the rock is exposed. On and between the rocks where debris accumulates, mats of *Cladonia rangiferina* (L.) Web. and *C. uncialis* (L.) Web. are common and frequently associated with cushions of *Polytrichum ohioense, P. commune, Leucobryum glaucum,* and *Dicranum scoparium* which occur in pure or mixed aggregations. In these moss-lichen cushions, or where sufficient leaf litter accumulates, *Polypodium virginianum* and occasionally *Dryopteris marginalis* and *Aralia nudicaulis* are present. Birch seedlings are common on the cushions, as are also such shrubs as *Gaylussacia baccata, Vaccinium angustifolium, Kalmia latifolia,* and occasionally *Rhododendron maximum.* The trees which eventually become established grow with their roots spreading through the moss mats. However, as the roots increase in size and portions of the mat are eroded away, the roots become exposed. These roots of the larger trees frequently grow between the boulders. The trees, thus poorly anchored, frequently lean and often exhibit inferior growth form. On most rocky areas this succession long ago reached a forested stage resulting in many rocky woodlands in the park.

HYDRARCH SUCCESSION

Two patterns of hydrarch succession are evident in the park. In the artificial impoundments, filling is occuring primarily by sedimentation and by the invasion of emergent aquatic vegetation. In contrast, lakes of glacial origin are being filled by the encroachment of a floating mat upon which vegetation thrives and which deposits organic material from the under side. However, in both of these patterns, submerged and floating aquatics are present in the deeper water. In the two instances, the filling by encroachment of emergents or by mat formation, different types of forest communities result. In the former the forest is composed primarily of broad-leaved trees (swamp forest), in the latter of conifers and scattered broad-leaved species (bog forest) (Fig. 1).

Both of these successional patterns are found in the park area. The earlier stages of the succession may be observed in the five lakes and two beaver dams. Three of them, Steeny Kill Lake (No. 20), Saw Mill Pond (No. 21), and an unnamed pond (No. 22), are artificial impoundments (Fig. 1). In contrast Lake Marcia (No. 23), and Lost Lake (No. 24), are of glacial origin. Sussex reservoir (Lake Rutherford) although surrounded by park property was not studied.

HYDRARCH SUCCESSION WITHOUT A FLOATING MAT

Aquatic zonation is well illustrated at the southern end of Steeny Kill Lake (Fig. 6). The area occupied by the lake was formerly a swamp forest. The trees were cut and a dam built at the northern end. Stumps project above the water in the southern end of the lake; elsewhere the deeper water has submerged them. *Callitriche heterophylla* and species of *Potamogeton* are the predominant submerged forms. On the exposed stumps grow *Leersia oryzoides* and *Spiraea tomentosa.* In the shallower water, is an emergent zone dominated by *Sparganium americanum* which grows 1-2 ft. in height (Fig. 6). Its associates are *Iris versicolor, Leersia oryzoides* and several species of *Scirpus.* On hummocks in this zone Spiraea occurs with *Hypericum virginicum, H. mutilum* and *Galium tinctorium.* Further back *Juncus effusus* and *Scirpus cyperinus* become the principal species. Between the hummocks of Carices and *Osmunda cinnamomea,* Sphagnum forms a more or less continuous layer with scattered plants of *Drosera rotundifolia, Dryopteris thelypteris, Chrysosplenium americanum,* and *Scirpus atrocinctus.* Here and there

FIG. 6. Hydrarch succession at southern end of Steeny Kill Lake. Note concentric zones beginning with *Sparganium americanum* at edge of water and followed by Juncus-Scirpus stage, shrub stage, and finally swamp hardwoods community in left background.

are pure stands of *Typha latifolia* in the Juncus-Scirpus zone, especially near the shrub zone which is further back.

A shrub zone occurs next to the sedge zone and in it *Alnus rugosa, Ilex verticillata, Nemopanthus mucronata,* and *Vaccinium corymbosum* are predominant. Less important shrubs are *Rhododendron maximum* and *Rhus vernix.* The shrub layer is from 5 to 10 ft. in height. The wet, hummocky ground is covered with Sphagnum and herbs: *Polygonum sagittatum, Osmunda cinnamomea, Dryopteris thelypteris* and various species of *Carex.* Young trees of red maple (*Acer rubrum*) and gray birch (*Betula populifolia*) are especially common in some parts of the shrub zone.

At other places along the lake shore where the bottom gradient is steeper, the zonation is less conspicuous and somewhat telescoped. In places *Cephalanthus occidentalis* and *Scirpus validus* play an important part in the succession, but are scattered in their distribution.

In contrast, probably because of the rocky substratum, aquatic vegetation is poorly represented in Saw Mill Pond and Lake Marcia. In the former *Sparganium americanum* and *Brasenia schreberi* are sporadic along the shallow lake shores. At Lake Marcia, those plants which occur are restricted primarily to shallow inlets where mucky soil has accumulated. Here one may find patches of *Juncus effusus, J. acuminatus, Eriocaulon septangulare, Ludwigia palustris* and species of *Eleocharis.* Other species that have been found in Lake Marcia but contribute little to the vegetation are *Juncus canadensis, Scirpus validus,* and *Eleocharis palustris* (Renlund 1951). Along the rocky shores a dense shrub thicket has developed with *Vaccinium corymbosum, Rhododendron viscosum, Myrica gale, Celphalanthus occidentalis, Clethra alnifolia* and *Alnus rugosa* as the principal species.

In the southern sector of the park, a small shallow unnamed pond is surrounded by a dense shrub zone. At the eastern end on the exposed muddy substrate a willow thicket (*Salix sericea*) is dominant, giving way to Alnus toward the upland. In other places along the margin *Rhododendron viscosum, Ilex verticillata, Vaccinium corymbosum, Viburnum recognitum, Alnus serrulata, Alnus rugosa* and *Cephalanthus occidentalis* form a dense border. In the open water, herbaceous aquatics are relatively sparse. In the shallow water near the shore one finds a few scattered patches of *Ludwigia palustris.*

In the southern part of the park, beavers have built a dam, forming a pond in a low swampy area, and killing many swamp hardwood species. Along the pond margin *Typha latifolia* grows in sporadic clumps. On the surface of the water one frequently finds a dense covering of *Lemna minor.* In the central part of the park, beavers have recently flooded a low swampy area and the surrounding oak forest. Some of the trees are dead and others are dying either due to flooding or the activities of the beavers girdling the bases of the trees. Aquatic vegetation is sparse due to the recency of the disturbance; however, near the shore *Lemna minor* frequently covers the surface of the water.

Another area, at one time inundated by the activities of beavers and since abandoned, has been drained and today Big Flat Brook flows through it. The area shows evidence of having been pastured before flooding. After its use as a pasture ceased gray birch, red maple and hawthorn (*Crataegus* spp.) invaded. The flooding produced by beaver activities killed the birch and hawthorn. Since the withdrawal of water, a dense willow thicket now grows along much of the stream. Rushes, sedges, and grasses are also important along the stream and on the exposed lake bed along with species of *Eleocharis* and other herbs. In some areas the herbs give way to shrubs—*Viburnum dentatum, V. lentago, Lyonia ligustrina,* and *Alnus rugosa.*

All of these earlier stages in hydrarch succession appear to be leading toward a swamp hardwoods community. Stands representing this community occur in poorly drained areas, chiefly along the tributaries of Big Flat Brook. Here two stands (14, 15) were studied in detail (Fig. 1).

The forest floor is wet and boggy. In one stand (15) a mixture of woody, sedge, and sphagnum peat extends to a depth of 3 ft. This is underlain by yellow-brown sedge peat which gives way to gray clay at a depth of 9 ft.

The tree canopy is composed of two more or less distinct layers, below which is a sporadic shrub layer and fairly continuous herb and moss layers. In the tree layer, red maple and yellow birch (*Betula lutea*) are the dominant species, contributing up to 70% of the total tree cover in the two stands. In one stand, yellow birch is most important; whereas in the other, red maple is predominant. Associates are black ash (*Fraxinus nigra*), white ash (*Fraxinus americana*), basswood (*Tilia americana*), and tulip tree (*Liriodendron tulipifera*) (Fig. 6, 13). The tree canopy covers 94% of the total area. Most of the trees are 4-9.9 in. d.b.h. although larger ones attaining 16-18 in. d.b.h. are represented. In gen-

eral, the trees are shallowly rooted and somewhat elevated above the frequently water-filled depressions on the forest floor. The average height of the forest is 65 ft. In the understory hornbeam (*Carpinus caroliniana*) is most important, with hop hornbeam (*Ostrya virginiana*) and transgressives of the dominants. Yellow birch, red maple, white ash, and hop hornbeam are all reproducing themselves. Yellow birch seedlings are most abundant followed by red maple and white ash.

In the sparse shrub layer, covering 16% of the total area, there is considerable variation. In one stand (14) *Hamamelis virginiana* and *Vaccinium corymbosum* contribute 71% of the total shrub cover. In the other (15) *Viburnum dentatum* and *Viburnum lentago* contribute 57%. Shrubs present in both stands are listed in figure 14.

The herb layer is relatively continuous, covering about 70% of the area. The three most important herbs in each stand are *Osmunda cinnamomea* with a 33% contribution to the cover, *Carex stricta* with 29%, and *Symplocarpus foetidus* with 5%. Carex and Osmunda form characteristic hummocks on the forest floor with Sphagnum occupying the wetter depressions between them. Other herbs are listed in figure 15.

Bryophytes occupy 31% of the area. Sphagnum is most important, contributing about 21% cover. Others, in order of decreasing importance, include *Thuidium delicatulum*, *Mnium punctatum* var. *elatum*, *Mnium cinclidioides*, *Tetrapis pellucida*, *Dicranum scoparium*, *Bazzania trilobata* and *Trichocolea tomentella*. They are usually found on the elevated tree roots and sedge hummocks.

Near Lake Rutherford the swamp hardwoods community occurs with red maple, black gum (*Nyssa sylvatica*), and sporadic white pine which towers above the deciduous species. *Vaccinium corymbosum*, *Rhododendron viscosum*, *Alnus rugosa*, and *A. serrulata* are the dominant shrubs there and gray birch forms a conspicuous border. Frequently hemlock (*Tsuga canadensis*) and black gum are mixed in with the other broad-leaved species as at the northern and southern ends of Steeny Kill Lake. In other poorly drained areas, swamp-white oak (*Quercus bicolor*) is also present.

HYDRARCH SUCCESSION WITH A FLOATING MAT

The second pattern of hydrarch succession is associated with the formation of a floating mat. This is best illustrated by Pine Bog (locally referred to as Pine Swamp) located on the southwestern boundary of the park, 1200 ft. above sea level (Fig. 1, No. 25). It was formed as a result of glacial drift blocking the drainage of a mountain valley (Waksman, *et al* 1943). In the southern part of the bog, an open body of water (Lost Lake) is surrounded by a floating sedge and sphagnum mat (Fig. 7). On the mat, *Chamaedaphne calyculata* is the dominant shrub and along with it are *Andromeda glaucophylla*, *Kalmia polifolia*, *K. angustifolia*, and *Vaccinium oxycoccos*. Here small trees of black spruce (*Picea mariana*) and

FIG. 7. Lost Lake in Pine Bog surrounded by a floating mat on which *Chamaedaphne calyculata* is the dominant species. Tamarack and black spruce in foreground. Peat samples were taken on the opposite side of the lake where the person is standing.

tamarack (*Larix laricina*) have been seeded in from the surrounding tree and shrub zone. The tamarack is restricted primarily to the open mat; the black spruce is not only on the mat but throughout the greater portion of the more mature bog. Along with black spruce, red maple, black gum, yellow birch and sporadic white pine and hemlock form a very open forest rising above a dense shrub layer. The shrubs are mostly *Vaccinium corymbosum*, *Rhododendron viscosum*, *Alnus rugosa* and species of *Ilex*. *Rhododendron maximum* forms a border along the edge of the bog.

A later stage in bog succession is illustrated by Cedar Bog (locally called Cedar Swamp), which is located at the northern park boundary approximately 1500 ft. above sea level (Fig. 1 Stand 19). It is probable that this was a lake that filled in the same way as Pine Bog. However, the encroachment on the lake is complete and no open water remains. The area is now completely covered by a forest of coniferous and deciduous species. Although it is mostly a rather closed forest, the southwest portion is like much of Pine Bog with red maple, yellow birch, black gum and occasionally white pine and black spruce, scattered throughout a shrubby matrix.

Where the bog forest is most mature (Stand 19) it consists of distinct tree, shrub and moss layers. There are very few herbs. In the tree canopy, hemlock and red maple are dominant, contributing 55% of the total tree cover. Other trees contributing cover are southern white cedar (*Chamaecyparis thyoides*) with 14% cover, yellow birch 12%, black spruce 10% and black gum 9% (Fig. 8, 21). Cover in the tree layer is 89% with only 11% represented by openings in the canopy. The larger hemlocks and cedars are approximately 90 and 140 years of age respectively. The tops of many cedars and hemlocks are broken or dying back as a result of wind and ice storms. Others, especially hemlock, are branched on the side opposite the prevailing winds. Windfalls are occasionally found with the shallow root systems of the fallen trees tipped up on edge. Logs in various stages of decomposition furnish an excellent substrate for establishment of seedlings. Dead stand-

FIG. 8. Cedar Bog. Crowns of *Chamaecyparis thyoides* most conspicuous. Road crosses bog at this point. Young cedars are common along the road.

ing trees, especially cedars, are scattered throughout; one cedar measured 25" d.b.h. Some cedars up to 30" in diameter have been cut.

The trees differ in their ability to complete their life cycle. Hemlock and red maple are most successful. Cedar seedlings are sparse except in the openings. Those that become established in dense shade usually die when 3-4 in. in height. Cedar is destined to be of less importance in the future as a result of competition from the more shade tolerant hemlock and red maple. Only locally is it increasing in importance. For example, along a road recently constructed across the bog, white cedar shows vigorous reproduction with an abundance of seedlings and saplings and larger trees 3-4 in. d.b.h. Black spruce reproduction is also poorly represented, it, like the cedar being more important in the less mature parts of the bog. Reproduction of yellow birch and black gum indicates that they will maintain their present status in the community.

The shrub layer is 93% complete, there being only 7% of the area unoccupied. Of this shrub cover, *Rhododendron maximum*, which occurs primarily in deeper shade, forms a dense undergrowth contributing 64%. Its seedlings are abundant on the moss-covered hummocks and root systems. The remaining 36% of the shrub cover is contributed by *Ilex laevigata, I. verticillata, Nemopanthus mucronata, Vaccinium corymbosum* and *Alnus serrulata* which occur primarily in the openings. In the southwest portion of the bog where it is more open *Rhododendron maximum* frequently decreases in importance. Here in addition to those shrubs previously mentioned *Rhododendron viscosum, Alnus rugosa* and *Lindera benzoin* form an almost continuous shrub layer.

In the mature forest, herbs are widely scattered. *Osmunda cinnamomea* contributes 5% cover, *Calla palustris* 3%, and *Symplocarpus foetidus* 1%. These are most important in the openings. Of the remaining 13 herbs each contributes less than 1% cover. Beneath the shrubby matrix in the more open portions of the bog, tussocks of *Osmunda cinnamomea* covered with Sphagnum are characteristic. Along the road across the bog, Sphagnum supports a distinctive herbaceous flora including species such as *Calla palustris, Sarracenia purpurea, Drosera rotundifolia, Scirpus cyperinus, Eriophorum* sp., *Juncus effusus* and species of *Carex* and *Eleocharis*.

DEPOSITS OF PINE BOG AND CEDAR BOG

Samples of the sediments now filling the lake basins of Pine and Cedar Bogs were obtained to a depth of 40 ft. and 30 ft. respectively. In the lowest levels, the deposits consist of 8-10 ft. of gray clay. These are overlain by gyttja which is formed in the open lake waters as a result of benthic fauna reworking planktogenic detritus (Lindeman 1941). The gyttja varies from fine detritus ooze in the lower levels to coarse detritus ooze in the upper levels (Deevey 1939). Its depth ranges from 10-15 ft. in the two bogs. The upper layers of sedge and sphagnum peat were formed by dead material of sphagnum, sedges, and associated plants falling from the underside of the mat. As this is continuously built up by fresh deposits, it compresses the underlying gyttja. In Pine Bog 17 ft. of sedge-sphagnum peat has accumulated. In Cedar Bog there are 4 ft. of sedge peat containing fragments of wood, overlain by 6 ft. of woody peat.

ABANDONED FIELDS

Most of the former farm land is now abandoned to the invasion of native vegetation, and various successional stages are evident leading to an oak or oak-hickory forest community (Fig. 1). Along the lower southeast escarpment, on the Martinsburg shale, abandoned fields are more or less continuous. Erosion there has removed much of the glacial drift, exposing the shale so that the vegetation there is directly influenced by the underlying geological formation. On the High Falls and Shawangunk formations, throughout the rest of the park, the old fields are more scattered. Where there are old fields, glacial drift covers the bed rock. Agricultural use of the land has ceased, except for several fields seeded with timothy and clover a few years ago and still mowed each summer.

PERENNIAL HERBACEOUS STAGE

There are no fields just abandoned, but on those with good drainage in which cultivation has most recently ceased, *Poa compressa, Daucus carota, Solidago graminifolia*, and *Hypericum perforatum* are the dominants (Fig. 9). Next in importance are *Hieracium pratense, H. aurantiacum, Trifolium pratense, T. repens, Linaria vulgaris, Agrostis alba, Phleum pratense*, and about 34 other herbaceous species scattered through the vegetation. *Andropogon scoparius* is not very important in the succession except in fields whose soils are derived from the shale. Fields in this early stage of succession are commonly bordered by hedgerows of gray birch, trembling aspen (*Populus tremuloides*), black cherry (*Prunus serotina*), scarlet oak (*Quercus coccinea*), and red maple (Fig. 9). From this border the trees spread out into the field and one finds young plants among the herbs near the edge of the field.

In the southern part of the park on the poorly

FIG. 9. Perennial herbaceous stage. *Daucus carota* and *Solidago graminifolia* are dominant herbs. Gray birch and trembling aspen at left and oaks at right form border along hedgerow.

drained Papakating silt loam, *Potentilla simplex, Iris versicolor* and species of *Carex, Juncus, Solidago,* and *Agrostis* are dominant in the fields that have not been plowed for some time. Other species present are *Linaria vulgaris, Hypericum perforatum, Cirsium arvense* and *Phleum pratense.* Woody species of *Spiraea* and *Clethra* are invading this community.

THICKET STAGE

Gray birch spreads out over most fields relatively fast (Fig. 9). Along with it appear the shrubs—*Rhus typhina, R. glabra, Quercus ilicifolia* (scrub oak), *Rubus* spp. and various heaths. The herbs of this thicket stage are primarily *Agrostis alba, Potentilla simplex, Solidago graminifolia, Hypericum perforatum, Linaria vulgaris, Solidago rugosa* and *Poa compressa.* As the succession continues considerable variation is evident. Gray birch may form a relatively uniform and continuous, tree layer growing in clumps and ranging from 1-4 in. d. b. h. With it may be found scattered black cherry, red maple, and white ash as well as saplings of red oak (*Quercus rubra*), white oak (*Quercus alba*), red maple, and scarlet oak. Species of *Rubus* commonly form a dense tangle 3-4 ft. in height. The dominant herbs are *Solidago rugosa* and *Potentilla simplex.*

On the other hand, gray birch and red maple may be co-dominant in which case the shrub layer may consist of *Quercus ilicifolia, Vaccinium angustifolium, V. stamineum, Viburnum recognitum, Hamamelis virginiana* and species of *Rubus.* In such stands *Lycopodium complanatum* and *Polytrichum commune* frequently form continuous mats over the ground. Where rock outcrops in the thicket, *Polytrichum commune, P. juniperinum* and *Danthonia spicata* cover the area. Sometimes white pine and pitch pine (*Pinus rigida*) are associated with red maple and gray birch. Saplings of hickory (*Carya* spp. including *C. glabra* and *C. ovalis; Carya ovata*) red, white, scarlet, and black oak (*Quercus velutina*) are also common. On the Martinsburg shale red cedar (*Juniperus virginiana*) is occasionally associated with gray birch and red maple but does not occur in the other areas.

FOREST STAGE

Eventually a forest of oak or of one dominated by oak and hickory gains ascendancy over the birch (Fig. 10). Some of the same shrubs found in the thicket persist but there is a change in the herb composition. The principal ones are *Lycopodium complanatum, Pteridium aquilinum, Lysimachia quadrifolia,* and *Medeola virginiana.* The resulting forest is dominated by either red oak, chestnut oak, white oak and hickory or by white oak and hickory alone.

FIG. 10. Approaching forest stage. Gray birch and pitch pine still present. Larger trees are oaks.

Other trees common in the young forest are black oak, red maple, and scarlet oak.

PITCH PINE-OAK COMMUNITIES

The pitch pine-oak communities occur on the Shawangunk conglomerate as a depauperate pine-scrub oak community (Fig. 11) and on the drift overlying the High Falls sandstone as a pitch pine-arborescent oak community. Four stands of the pine-oak community were studied, two (Stands 1, 2) on the Shawangunk conglomerate and two (Stands 3, 4) on the High Falls sandstone. The former will be referred to as the pine-scrub oak and the latter as the pine-oak.

FIG. 11. Pitch pine-scrub oak community. Note heaths in crevices of conglomerate. Chestnut oak community is contiguous with pitch pine at right (Stand 2).

PINE-SCRUB OAK

On the ridge where the pine-scrub oak community occurs, the soil is very thin and rock outcrops are common (Fig. 11). Often mats consisting primarily of organic material bound together with roots cover the rock surfaces. The pH is approximately 4.

The tree and herbaceous layers are open, in contrast to a shrub layer that furnishes practically com-

plete cover (Fig. 13, 14, 15). The pitch pines, the dominant trees contributing 76% of the total tree cover, are rather widely spaced. Species associated with the pine in order of decreasing importance are red maple, gray birch, juneberry (*Amelanchier arborea, A. laevis*), and sweet birch. The tree layer averages 18-20 ft. in height with the larger pines 8-10 in. d. b. h. and approximately 70 years of age. The pines typically have broken tops or tops with gnarled or twisted branches. The open aspect of the woods is evidenced by the 54% unoccupied space in the tree layer (Fig. 13).

Pine seedlings and saplings are occasionally found in the rock crevices or moss mats where sufficient soil is present. Seedlings of red maple are frequently found. Saplings of sassafras (*Sassafras albidum*), juneberry, red maple, and sweet birch are scattered throughout the stands. Although a chestnut oak community always borders it, chestnut oak saplings are rarely found in the pitch pine community of the ridge top.

The shrubs are conspicuously two-layered, covering 92% of the area. The taller shrubs are scrub oaks which often form a dense thicket 3-10 ft. high. The lower layer is dominated by heaths, of which *Vaccinium angustifolium* and *Gaylussacia baccata*, typically two feet or less in height, are most important contributing 57% cover. Low shrubs of less importance are *Pyrus melanocarpa, Vaccinium vacillans, Kalmia angustifolia, Amelanchier stolonifera* and *Comptonia peregrina, Diervilla lonicera, Prunus pensylvanica, P. pumila, Rhus copallina,* and *Pyrus americana*.

The herb layer, in contrast, covers about 20% of the ground. Of the 21 species of herbs *Maianthemum canadense, Pteridium aquilinum,* and *Aralia nudicaulis* together contribute approximately 20% cover in this layer. All the others contribute a total of less than 1%. The moss layer is sparse covering less than 1% of the area.

Evidence of browsing by deer is conspicuous. Plants most frequently browsed include pitch pine, sassafras, juneberry, mountain ash saplings and certain herbaceous species. Evidence of fire in the recent past is indicated by the fire scars on the base of the tree trunks.

PINE-OAK

The pine-oak occurs on some of the hilltops of the High Falls formation. The soil is a podzol, the A horizon ash-gray in color underlain by a yellow-brown B horizon. The pH of the soil is about 4.5.

The tree canopy frequently consists of two more or less distinct layers. The uppermost layer is dominated by occasional pitch pine extending 10-15 ft. above the lower oak canopy. The pitch pine contributes approximately 24% cover. The deciduous lower layer of red maple, scarlet (*Quercus coccinea*), white, and chestnut oaks represents about 65% of the total tree cover (Fig. 13). Trees of minor importance are black gum (*Nyssa sylvatica*), black oak (*Quercus velutina*) and sassafras. There is about 20% unoccupied space in the tree layer compared to about 50% in the pine-scrub oak community of the ridge top (Fig. 13). The larger pines are 17-19 in. d. b. h. and about 140 years of age. Most of them are over 10 in. d. b. h. The hardwoods are most abundant in the small size classes. Pine snags and rotting pine logs occasionally are present. White oak, scarlet oak, chestnut oak, and red maple are reproducing, and chestnut sprouts are present. Pine seedlings are rare and saplings are completely absent.

In the shrub layer, *Gaylussacia baccata* is dominant, contributing about 60% of the cover. Other heaths represented are similar to those found on the ridge (Fig. 14). Scrub oak contributes about 15% of the cover and occurs in clumps, where ample light reaches it. The shrub layer is rather dense, covering about 85% of the area.

Ten herbs were found. They occupy only about 15% of the area (Fig. 15). *Pteridium aquilinum* has an average of 9% cover. None of the others furnish over 1% cover. Principal among them are *Gaultheria procumbens, Aralia nudicaulis,* and *Medeola virginiana*. Mosses occupy less than 1% of the area.

CHESTNUT OAK COMMUNITY

The chestnut oak community is the characteristic community of the park. It forms a matrix in which all the other communities are found (Fig. 1). A total of 6 stands was studied. Four (5, 6, 7, 10) of the stands were selected on the Shawangunk formation; two (5, 10) on the southeast escarpment below the monument; another (6) on the northwest slope above Cedar Bog and the remaining (7) on the ridge above, where it occupies a slight depression. The two stands on the High Falls (8, 9) are located on gently undulating topography overlain by glacial deposits (Fig. 1).

On the upper and mid-slopes and many sites along the ridge top of conglomerate where the soil is very rocky, the most xeric aspect of the chestnut oak community is characteristic (5, 6). Here an organic layer consisting of 3-6 cm of leaf litter overlies a mor humus layer which forms a mat over the rocky substratum. Depressions along the ridge top, filled with soil, constitute a more favorable environment for this community (7). An especially favorable site for the community is on the High Falls formation where the soil is relatively deep overlying the bed rock (8, 9). On the lower slopes, although the ground is very rocky, the interstices are filled with finer soil resulting in an even more favorable soil mantle than upon the slopes and ridge tops (10). In this community the soil pH is 5.0.

Within the chestnut oak community, there is a progression from the most xerophytic aspect (5, 6) (Fig. 12), to the deeper soils, especially on the High Falls and depressions on the ridge top (7, 8, 9), to the lower slopes of the conglomerate which represent the most mesophytic phase (10) (Fig. 13, 14, 15).

On the rocky slopes, the forest consists of two more or less distinct tree layers, a relatively continuous shrub layer and sparse herb and moss layers.

FIG. 12. Chestnut oak community along road to Cedar Bog. The most xeric aspect characteristic on rocky slopes.

In the tree layer, chestnut oak is by far the most important, contributing over 55% of the total cover. The principal associate is red oak. Black oak and sweet birch are occasionally present. Although the total cover in the tree layer is over 90%, the tree crowns are thin, transmitting a considerable amount of light.

Most of the trees fall into 1-3.9 in. and 4-9.9 in. size classes, but larger specimens are scattered throughout the stand. Two or more trees growing

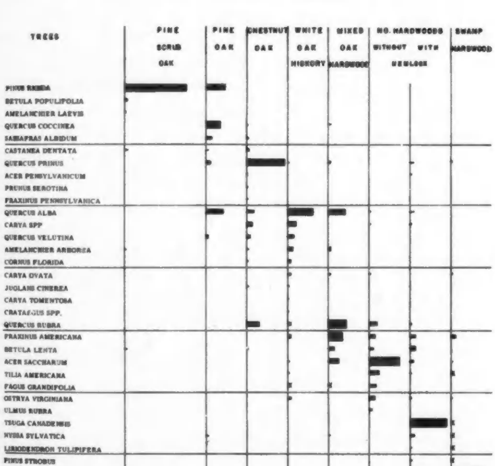

FIG. 13. Tree cover and frequency for forest communities. Length of bar represents % of total cover, width of bar represents % frequency of occurrence on 20 m segments along the transect lines in all stands sampled of each community. For example, in the pine-scrub oak community *Pinus rigida* is dominant contributing 76% of the total tree cover and representing 93% frequency. The (X) indicates that the species was present in the community but not occurring on the transects. Space refers to the portion of the canopy between the crowns of the trees. For example, in the pine-scrub oak community, where the gaps in the canopy are greatest, space is equal to 54% of the total area, in contrast with the mixed oak-hardwoods where the canopy is completely closed. *Carya* spp. include *C. glabra* and *C ovalis.*

from a single root system are common. The larger chestnut oak are 9-14 in. d. b. h. and approximately 95 years of age.

The average height of the forest is 50 ft. The understory consists of red maple, sassafras, chestnut sprouts, and young trees of hickory and oak. All species are reproducing themselves although chestnut oak is most successful. Oak reproduction is primarily of sprout origin. Chestnut sprouts are common. Numerous fire scarred chestnut snags litter the forest floor.

The shrub layer covers 40% of the area. The uniform distribution of shrub stems forms a fairly continuous layer. In one stand *Gaylussacia baccata* and *Vaccinium vacillans* are most important, whereas, in the other *Kalmia latifolia* and *Rhododendron nudiflorum* predominate. Other shrubs of importance include *Vaccinium angustifolium* and *Kalmia angustifolia.* Of the 12 shrubs present 7 are ericads which furnish over 90% of the cover in this layer.

The herb layer is extremely sparse, the total cover in this layer being less than 10%. Of the 17 species present in the herb layer only two, *Aralia nudicaulis* and the sub-shrub *Gaultheria procumbens,* were estimated as contributing more than 1% cover. Others occasionally present are *Carex pensylvanica, Pteridium aquilinum* and *Melampyrum lineare.* Mosses contribute approximately 2% cover. The principal species, *Polytrichum ohioense* and *Leucobryum glaucum* frequently occur between exposed rocks where the leaf litter is relatively thin or absent.

This xeric phase extends onto the ridge tops wherever the soil is very rocky. Here the trees are smaller with low gnarled branches. They frequently occur in clumps of 3-6 from a single root system. In addition to the characteristic ericaceous shrub layer, clumps of scrub oak occupy the openings in the tree canopy.

On the ridge top where considerable drift has been deposited in the depressions (7) and over most of the undulating topography of the High Falls (8, 9) where the soil is relatively deep, oaks such as white, red, and black are associated with the chestnut oak.

On these more favorable sites chestnut oak contributes about 43% cover while its associates contribute 24%. The trees fall primarily into the 1-3.9 in. and 4-9.9 in. size classes except on the High Falls where the 10 in. or over size class is of equal or greater importance. The larger trees on the ridge are 8-9 in. d. b. h. and 60-70 years of age while those on the High Falls are 15-16 in. d. b. h. and 110 years old. The average height of the forest is 45 ft. on the ridge and 65 ft. in the High Falls stands.

A distinct understory of red maple and oak transgressives contributes the greatest cover in the understory although sassafras, hickory, and juneberry are also present. All species appear to be reproducing themselves, yet most of the reproduction is of sprout origin. Chestnut sprouts are common. Many hickory saplings exhibit inferior growth due to the dying back of the terminal buds. Many of the larger

FIG. 14. Shrub cover and frequency for forest communities. For explanation see legend for figure 13. *Rhododendron roseum* is present in chestnut oak community but it was not recorded in the transect data.

chestnut oaks are not healthy, and in fact dead trees are occasionally found throughout the stand.

The shrub layer is more or less continuous, but considerable variation occurs among the dominants in the different stands. The total cover contributed by the shrubs in approximately 56%. On the ridge, *Vaccinium angustifolium* and *Gaylussacia baccata* contribute over 80% of the shrub cover, whereas on the High Falls the latter, and *Vaccinium vacillans* occupy over 75% of the area. Other shrubs represented included *Rhododendron nudiflorum, Vaccinium stamineum* and *Kalmia angustifolium.* As in the previous stands, ericads contribute over 90% to the shrub cover.

The herbaceous layer is sporadically developed. A total of 29 herbs occupy less than 7% of the area. *Aralia nudicaulis, Carex pensylvanica, Pteridium aquilinum* are the only species representing over 1% cover. Those present in all stands are *Aralia nudicaulis, Uvularia sessilifolia, Lysimachia quadrifolia,* and *Hypoxis hirsuta.*

The mosses are restricted to rocky outcrops and the bases of tree trunks. Between the rock outcrops *Polytrichum ohioense, Leucobryum glaucum* and *Dicranum scoparium* are most important. *Thelia asprella, Leucobryum glaucum* and occasionally *Rhodobryum roseum* cover the bases of tree trunks, especially those of white oak.

On the lower slopes of the conglomerate where the soils are more continuous, red oak and hickory are associates with the chestnut oak (10). Together these species with the chestnut oak contribute 80% of the total tree cover. Other associates of minor importance are red maple, black oak, sweet birch, black cherry, butternut (*Juglans cinerea*) and red ash (*Fraxinus pensylvanica*). On these better sites the tree canopy contributes 97% cover in contrast to 90% on the upper slopes. The larger trees are chiefly oaks ranging from 17-23 in. d. b. h. Red oak exhibits the best growth with straight boles and well developed crowns. In contrast, the larger hickories frequently are somewhat decayed at the base and the tops are often broken. The average height of the forest is 60 ft. as compared to 50 ft. further up the slope.

The understory is similar to the poorer stands except for the pronounced increase in hickory transgressives and the presence of flowering dogwood (*Cornus florida*) and striped maple. Hickory, chestnut oak, and red maple are reproducing themselves, with hickory most abundant. Saplings of ash and sweet birch are present. Sprouts of sassafras and chestnut are common. Red oak is absent in the seedling class but present in all other size classes. Hickory and chestnut oak are the only species in all size classes.

The shrub layer covers 50% of the area. Of the 12 shrubs present *Cornus rugosa* contributes 62% of the cover. Others of less importance are *Corylus cornuta, Vaccinium vacillans, V. stamineum, Cornus alternifolia,* and species of *Rubus.* Two vines, *Parthenocissus quinquefolia* and *Vitis aestivalis,* contribute 9% and 4% cover respectively.

The herbaceous layer covers only 12% of the area. Of the 30 species represented not one contributes over 1% cover. *Collinsonia canadensis, Solidago caesia, Desmodium nudiflorum,* and *Smilacina racemosa* contribute a total of 3% cover. Other herbs, in order of decreasing importance, include *Amphicarpa bracteata, Uvularia perfoliata* and *Galium lanceolatum.*

In considering the three aspects of this community, chestnut oak is the characteristic species and along with it are varying amounts of red oak, white oak, black oak, red maple, and hickory (Fig. 13). The shrub layer is typically ericaceous with *Gaylussacia baccata, Vaccinium angustifolium,* and *Vaccinium vacillans* most common (Fig. 14). Those herbs which contribute the greatest cover are *Aralia nudicaulis* and *Pteridium aquilinum* (Fig. 15).

WHITE OAK-HICKORY COMMUNITY

The white oak-hickory community is characteristic in the wide valley floors along Big Flat Brook, on the moister upland sites of the High Falls Formation (Fig. 16), and occasionally in the later stages of old field succession. Two stands representing this community were studied in detail, one (No. 11) located near Big Flat Brook in the southern portion of the park, the other (No. 12) on a moist southeast facing slope above Big Flat Brook (Fig. 1).

In both stands the soil is rocky. A thin mor humus overlies a grayish-black A horizon which blends into a yellow-brown layer, the B horizon. The soil pH is approximately 5.

In this community, the forest consists of two more or less distinct tree layers, a shrub layer, and sparse herb and moss layers (Fig. 13, 14, 15). In the tree layer, white oak contributes about 32% and hickory

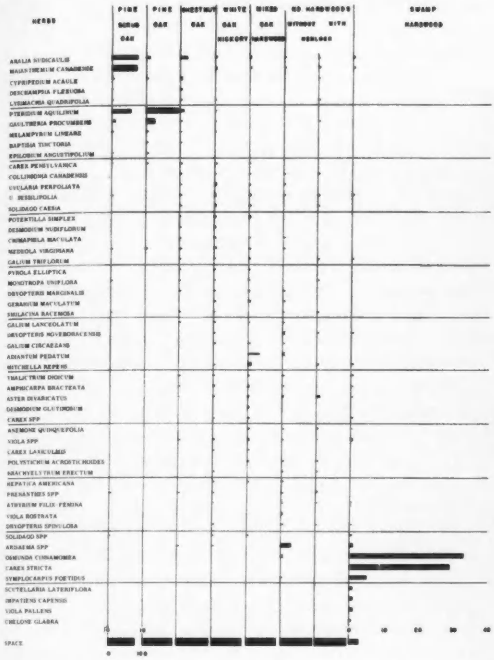

FIG. 15. Herb cover and frequency for forest communities. Length of bar represents % cover contributed by each species and the width of the bar represents the frequency of occurrence based on the total number of herb quadrats in all stands sampled of each community. The (X) indicates that the species was present in the community but not occurring in the quadrats. Space represents the amount of unoccupied area in the herbaceous layer.

about 15% of the total tree cover (Fig. 16). The importance of hickory varies considerably throughout the community. Other associates are black oak, red maple and beech (*Fagus grandifolia*). Sugar maple (*Acer saccharum*) and yellow birch frequently border the streams where they flow through this community. Sugar maple and white ash are most abundant in the smaller 1-3.9 in. size class, whereas white oak, hickory and black oak are most common in the larger size classes. The trees are tall and straight. There is no evidence of sprout origin. The height and diameter of a few of the larger trees are white oak, 26.7 in. d. b. h. (85 ft.), hickory (*Carya glabra*) 20.9 in. (80 ft.) and black oak 15.8 in. (74 ft.) (Stand 12). Chestnut, hickory, and white oak logs are found on the forest floor in various stages of decomposition (Stand 12). Red maple, juneberry, dogwood, white ash, and young trees of the dominant species comprise the understory. Nearer the streams hornbeam and hop hornbeam increase in importance (Stand 11). The dominant trees are reproducing themselves. Both seedlings and saplings of sugar maple, birch, and white ash are common (Stand 11).

About ⅓ of the shrub layer is occupied by shrubs. *Corylus cornuta* contributes an average of 24% of

FIG. 16. White oak-hickory community along road to Life Camp in southern part of the park.

the cover, *Hamamelis virginiana* 17% of the cover and *Viburnum acerifolium* 16%. A few others present are listed in figure 14.

In the herbaceous layer a very small amount, about 1/10 of the area, is occupied. Of the 54 species present, none contributes more than 1% cover. Those most frequently found include *Uvularia perfoliata, U. sessilifolia, Potentilla simplex, Solidago caesia, Aralia nudicaulis* and *Maianthemum canadense* (Fig. 15).

The moss layer is poorly developed. On and between the rocks, *Dicranum scoparium, Thuidium delicatulum* and *Polytrichum ohioense* were estimated as contributing a cover of 4%.

MIXED OAK-HARDWOODS COMMUNITY

The broad sloping valleys between the ridges and hills are occupied by the mixed oak-hardwoods community (Fig. 1). A stand studied in detail representing this community is located above Saw Mill Pond on a gentle east facing slope (Fig. 1, Stand 13). The soil there is relatively rocky with an organic layer of 1-3 cm. This organic layer appears to be rapidly incorporated into the underlying soil. Moist spots are common, whose degree of mesophytism is dependent to some degree upon the drainage from the upper slopes.

The forest consists of two distinct tree layers, a shrub layer and sparse herb and moss layers. It is often difficult to designate a single dominant since many tree species contribute significantly to the canopy. Those represented contribute the following cover: white oak 21%, red oak 22%, white ash 17%, sugar maple 12% and red maple 9%. Other trees interspersed among these are shagbark hickory (*Carya ovata*), chestnut oak, scarlet oak, black gum and beech. Juneberry and young trees of the main canopy comprise the understory. The tree layer is continuous, with no gaps in the canopy (Fig. 13). The larger trees are 14-16 in. d. b. h. and attain a height of 65 ft. The dominant trees are reproducing themselves. The white and red oak, while most important in the tree layer, are less successful in the reproductive stages. Red maple, sugar maple and white ash are reproducing prolifically.

The sparsely developed shrub layer contributes a total of only 24% cover. Among those represented, *Corylus cornuta* contributes 42% of the cover, *Hamamelis virginiana* 35%, and *Viburnum acerifolium* 16%. Others of less importance are listed in figure 14.

In the herb layer, 38 species contribute 13% cover (Fig. 15). Those contributing most to the cover are *Adiantum pedatum* with 3% and *Mitchella repens* with 1%. Others commonly present are listed in figure 15. Mosses cover only 1% of the area. They occur on the moist exposed soil and between the outcropping rocks. *Thuidium delicatulum* and *Polytrichum ohioense* are most common.

Northern Hardwoods Communities

Northern Hardwoods without Hemlock

The northern hardwoods community without hemlock is very restricted in its distribution in the park (Fig. 1.) The best stand is located in a narrow rocky valley in the southern portion of the park (Stand 16, Fig. 17). The ground consists mostly of rounded boulders which are often covered with an organic layer. In places on the valley floor, the boulders are exposed, since the organic material is frequently washed away by spring flood waters. Where not subjected to such flooding, the humus layer is 2-3 cm in thickness covering the rocky surface. Where soil is present among the rocks, it consists of a fine light yellow-brown clay loam with a pH of about 5.0.

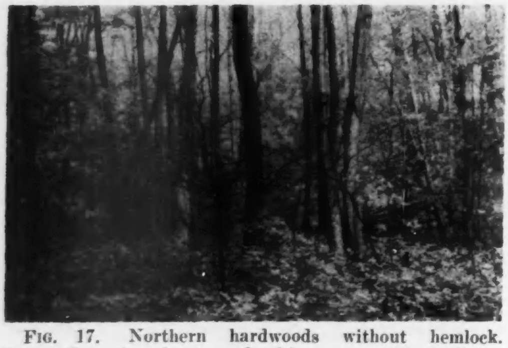

FIG. 17. Northern hardwoods without hemlock. Forest floor densely covered with sugar maple saplings. (Stand 16.)

The forest is composed of two distinct tree layers and sparse shrub and herb layers. The tree canopy is nearly complete with very few openings. Most of the trees are tall and straight. In the upper story are sugar maple and its associates—basswood, red oak, beech, yellow birch, white oak and sweet birch (Fig. 13). Locally beech and sugar maple are most important. Large sporadic white pine towering above the other trees are sometimes present. Chestnut was formerly an important element as indicated by the huge logs on the forest floor. Yellow birch is restricted primarily to the stream margins. The dominant trees vary from 75 to 94 ft. in height; for example one sugar maple 29 in. d.b.h. measured 94 ft., a basswood 12.4 in. 73 ft.; and a white ash 19.4 in., 75 ft. Hornbeam and hop hornbeam with young sugar maples constitute a sub-canopy layer. The trees differ in their reproductive potential. Sugar maple is abundantly reproducing itself (Fig. 17). Small plants 1-2 ft. in height are most common, a total of 784 such individuals were recorded in 400 sq. meters. Yellow birch seedlings are abundant, but saplings are absent. Basswood reproduction is relatively sparse, and beech is reproducing chiefly by root sprouts. White ash reproduction is important in both seedling and sapling stages.

The shrub layer is sparse, occupying only 14% of the total area (Fig. 14). To this 14% cover, *Lindera benzoin* contributes 46%. The other 5 species in order of decreasing importance are *Hamamelis virginiana* with 24% of the cover, *Viburnum acerifolium* with 18%, *Parthenocissus quinquefolia* with 7%, *Rhus radicans* with 3%, and *Corylus cornuta* with 2%.

The herbaceous layer is also sparsely developed, only 9% of the area being occupied. The two most important species are *Arisaema* sp. with 3% cover and *Symplocarpus foetidus* with 1%. Of the thirty-five others that occur, those most frequently present are listed in figure 15. Those present but not recorded in the quadrats are *Allium tricoccum*, *Adiantum pedatum*, *Osmunda cinnamomea*, *O. claytoniana* and *Dryopteris noveboracensis*.

The moss layer covers 2% of the area. Those most common on the rocks are *Thuidium delicatulum*, *Dicranum fulvum* and *Grimmia apocarpa*.

Northern Hardwoods with Hemlock

The northern hardwoods community with hemlock present is also restricted in its distribution. It occupies steep bouldery ravines (Stand 17) and low islands between streams (Stand 18). One stand studied in detail is located in the northwestern part of the park and another is situated ¾ mi. south of Saw Mill Pond.

The soil of the two sites varies considerably. On the steep, rocky, ravines, it consists chiefly of organic material which accumulates between the boulders. However, some of the accumulating humus is con-

stantly removed by flood waters in the narrow ravines and by erosion on the steep slopes.

An exception to this occurs just outside the park, east of Lake Marcia. There a stand lies at the base of the southeast escarpment on a north facing slope, where the conglomerate gives way to the underlying shale. At this point a stream has cut a deep ravine. The soil in this hemlock stand is derived from the shale and is relatively free of rocks. Where the community occurs on islands between streams, the soil is a rocky clay loam with a podzol profile. An organic layer overlies an ash gray A horizon (pH 4.2) below which is a yellow-brown B horizon (pH 4.8).

In the rocky ravines, hemlock and yellow birch are the important species, contributing 57% of the total cover of the forest canopy (Stand 17). Other main canopy associates in order of dominance are sweet birch, white ash, red maple, sugar maple, basswood, tulip tree, and white pine (Fig. 13). Hemlock is more important on the island sites and on the shale slope (Fig. 20). Here, along with the above associates, white oak, chestnut oak, and black gum may be present. The larger trees vary from 12 to 32.5 in. d. b. h. The larger hemlocks are 80-100 years old. The average height of the forest is 70 ft. An understory tree layer is poorly developed, with striped maple, hop hornbeam and transgressives of the dominant species contributing the most. All trees are reproducing, although oak is least successful. Hemlock and birch seedlings are most abundant. Occasionally hemlock seedlings are so abundant on the forest floor that they produce a green tinge. The seedlings of birch and hemlock occur chiefly on hemlock litter and on rotten logs. There is some evidence that this community may in time occupy a greater area, since in at least three stands, hemlock saplings are present not only within the stand, but also in the surrounding chestnut oak forest, as well as in abandoned fields and former pasture land.

The shrub layer of this community is relatively open, shrubs occupying not more than 25% of the area, usually less. Those shrubs which most frequently occur are *Hamamelis virginiana* and *Viburnum acerifolium* (Fig. 14). *Rhododendron maximum* is only locally important.

Herbs are sporadic occupying about 6% of the area. Those which are found most frequently include *Aster divaricatus, Maianthemum canadense, Trientalis borealis* and *Mitchella repens* (Fig. 15). *Lycopodium lucidulum* was present but it was not found in the quadrats.

Mosses cover 9% of the area in the moss layer, the rest being either litter or bare rock. Those present are *Hylocomium splendens, Dicranum scoparium, Climacium americanum, Mnium affine, M. punctatum,* and *Trichocolea tomentella.* In the stream flowing through one hemlock stand (17), are mats of *Eurhynchium rusciforme* and *Sematophyllum carolinianum* covering the rock surfaces.

POLLEN ANALYSIS

In general, the pollen record reveals an initial spruce-pine-fir-oak forest succeeded by a period of spruce-pine-fir and then a brief period of pine dominance. This was followed by a deciduous complex in which oak predominated. During the latter, two periods of hemlock maxima were separated by an intervening hickory maximum.

Although the two bogs show the same general trends, they do not correlate in the lower levels (Fig. 18, 19). Some of the records revealed in the bottom levels of the Pine Bog profile are absent in the profile obtained from Cedar Bog. What is especially conspicuous in the Cedar Bog profile, is the shortness of the spruce and fir record compared with

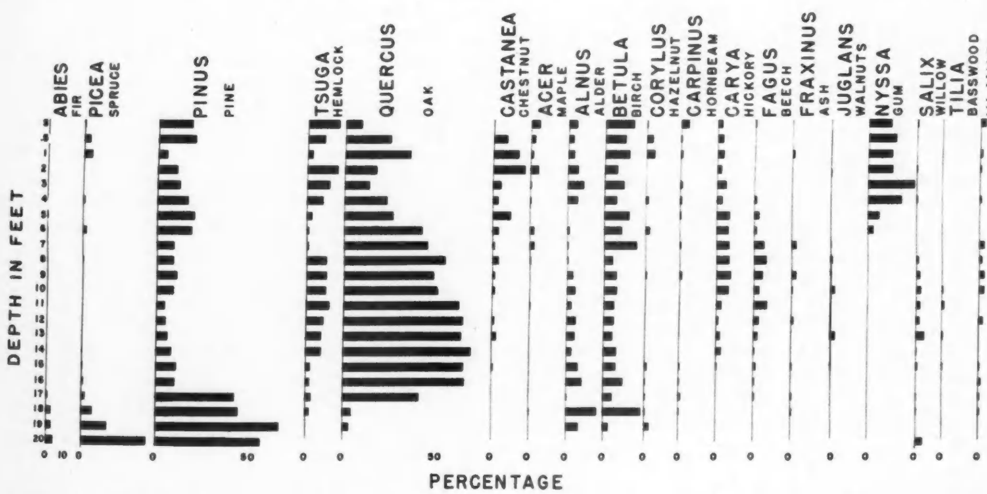

FIG. 18. Cedar Bog pollen spectrum. Length of the bar represents % of total tree pollen. For example, Pinus represents 18% at the surface(s) and 68% at the 19 ft. level. Chamaecyparis (cedar) is found only at the surface where it represents 10% of the total tree pollen.

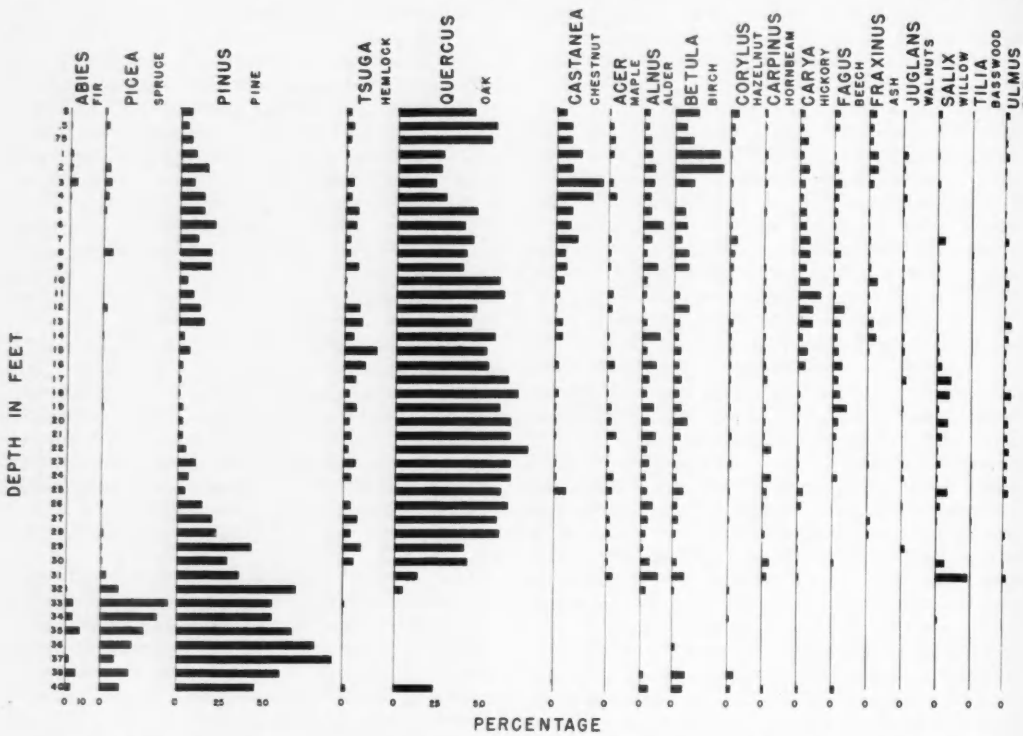

FIG. 19. Pine Bog pollen spectrum. Length of the bar represents % of total tree pollen. For example, Pinus represents 7% at the surface(s) and 46% at 40 ft. level. No pollen was found in the 39 ft. sample.

that of Pine Bog. In Cedar Bog, the 20 ft. level is comparable to the 33 ft. level in Pine Bog. The record found in the bottom 7 ft. from Pine Bog is absent from the Cedar Bog profile. Failure to find the deepest part of Cedar Bog may be the explanation for the incomplete profile there (Potzger & Wilson 1944). Although samples were obtained to a depth of 30 ft. in Cedar Bog, those from 21-30 ft. were sterile, except for a few pine and spruce pollen grains at about the 25 ft. level.

In the bottom levels (37-40 ft.) of Pine Bog, spruce, fir, pine and deciduous species occur. This is followed by a spruce maximum in which the deciduous element is practically absent. A pine period, which has been often shown to be very pronounced in eastern North America (Potzger & Otto 1943; Deevey 1939, 1943), if represented in these profiles was of short duration being recorded only in the 32 ft. level in Pine Bog and the 19 ft. level in Cedar Bog. This is succeeded by a long oak-hemlock-pine and mixed broadleaved period during which two hemlock maxima occurred. The first of these maxima (around the 15 ft. and 11 ft. level) is accompanied by a decrease in pine and oak. Between them, there occurred a period in which there was a decrease in hemlock and an unmistakable increase in hickory. The second hemlock maximum (5 ft. and 2 ft.) is accompanied by an increase in chestnut and spruce, and the reappearance of fir. Beech increased also during the hemlock maxima. Surface samples of Pine Bog, which presumably reflect the present day conditions, show oak and birch to be most important with a slight decline in pine and a rise in hemlock. In contrast, oak is much less important in Cedar Bog, where it is accompanied by an increase in hemlock, birch, maple and pine along with appearance of Nyssa and Chamaecyparis.

Small quantities of non-tree pollen were found throughout the profile. In the 1-4 ft. levels of Pine Bog, Compositae, especially Ambrosia, represents up to 20% and in the lower levels sedges and grasses were present. In the top levels of Cedar Bog, Chenopodium and Rumex occur.

DISCUSSION

That climate controls vegetation has long been recognized, the major vegetational patterns being determined by the regional climates (Tansley 1949; Weaver & Clements 1938). Within any region, one encounters plant communities whose presence and distribution are determined by local climate and edaphic conditions, as for example a ravine compared with an exposed ridge, or a site with a thin soil mantle over rock compared with a deep fertile soil. It is evident, therefore, that superimposed upon the

pervading influence of the regional climate are both physiographic and edaphic conditions which locally influence the vegetational pattern. Hence, in any regional vegetational pattern, there will be a matrix of vegetation in which the regional climate appears to have the principal control, but within which pronounced local variations occur. The whole pattern is subject to change as changes in the regional climate occur.

PAST VEGETATION

One might expect, as Transeau (1903) did, that tundra vegetation first occupied the area after the ice melted. However, no evidence for such was found, although Deevey (1951) reports pollen evidence of tundra vegetation being found in Maine and possibly in Connecticut bogs. The beginning of the record in Pine Bog shows the presence of deciduous species accompanied by pine and a low representation of spruce. This suggests a period of moderate climate at the start of the record. Since the area lies within the Cary moraine and about 100 mi. south of the Mankato moraine (P. MacClintock, personal communication) it suggests that considerable climatic amelioration occurred following the Cary. This was followed by a disappearance of the deciduous forest species and a spruce dominance which may be correlated with the readvance of the Mankato substage. Deevey (1939, 1943) found a similar fluctuation in Connecticut which he correlated with recession and advance of Early and Late Mankato substages. However, from recent studies in Maine, Deevey (1951) suggests a different interpretation. In these studies he considered the rise in spruce as recording the actual invasion of spruce into the region, but below the spruce maximum he considers the tree pollen wind-borne from a distance. However, this does not seem to be a likely interpretation at High Point State Park since there is a paucity of non-tree pollen.

Pine becomes important early in the profile, as compared with the vegetational sequences illustrated by profiles in the midwest; a phenomenon that may be the result of climate under more maritime conditions (Potzger & Otto 1943). Climatically the spruce-pine-fir period was cool and moist. The subsequent brief period of pine dominance suggests drier conditions (Sears 1948). It is of much shorter duration than the pine period recorded by most bogs studied in the Northeast: in New Jersey (Potzger & Otto 1943), in Connecticut (Deevey 1939, 1943, 1951) and in New Hampshire (Krauss & Kent 1944). However, it is comparable with Deevey's Linsley Pond (L-9 and L-10) profiles. Radiocarbon studies show the time of attainment of the pine period in North America to vary roughly with latitude. In West Virginia it was attained about 9,000 years ago, in Connecticut 8,000 and in Maine 6,000 years (Flint & Deevey 1951). Since these bogs are located relatively near Connecticut the pine period probably occurred around 8,000 years ago in northern New Jersey.

Following the pine period deciduous species, especially oak, rapidly became important and have persisted until the present. This change is suggestive of a warmer climate. Associated with these deciduous trees there appeared the hemlock. Its history is accented by two periods of greater importance. These two periods may be interpreted as times of increased moisture (Potter 1947). This interpretation is further strengthened by a correlated decrease in hickory at the hemlock maxima. Between the hemlock maxima a rise in hickory is indicative of drier and possibly warmer conditions. This level probably marks what has been known as the last xerothermic period which had widespread effects upon eastern North America (Sears 1942; Raup 1937; Transeau 1935; Gleason 1923). From samples obtained in Connecticut the date of the hickory maximum has been tentatively set by the radiocarbon method at about 1800 ± 500 years ago (Flint & Deevey 1951). The second hemlock maximum was accompanied by an increase in chestnut and a decline in hickory which together indicate a return to more mesic conditions. Evidence for such a shift is strengthened by the reappearance of spruce and fir.

And indication of the historical period is suggested toward the top of the profiles. In Pine Bog the local influence of a developing bog forest may to some extent mask the true picture of upland conditions. It is possible that the increase in pine near the top may be evidence of such an influence. The appellation Pine Swamp along with the presence of white pine and dead snags in the bog today would suggest that pine was probably more important in recent time than at present. The pronounced rise in birch accompanied by a decline in hemlock suggests the temporary dominance of gray birch as a result of fires and man's activity.

The surface levels of Pine Bog reflect the present upland vegetation dominated by oak and other deciduous species. Hemlock has increased slightly, but its still restricted distribution in the most mesic sites is reflected in the surface layers. In contrast in Cedar Bog, the upland forest is partly masked by the mature bog forest covering much of the bog today. This is shown by the increase in hemlock, birch, and maple along with the appearance of gum and cedar.

An interesting correlation results when Pine Bog is interpreted in terms of Sears (1948) suggested correlation between northeastern pollen profiles and climatic fluctuations since early Wisconsin time. The substage advances may be correlated with an increase in hemlock or spruce, and retreats with a rise in pine, or oak and hickory, concurrent with a decrease in hemlock or spruce. Beginning at the top of the profile, the low percentage of hemlock and higher percentage of oak may reflect the retreat of the Alpine-Alaskan, although the historical period with man's influence may be equally or more important. The increased importance of hemlock between the 3-9 ft. levels may be correlated with the Alpine-Alaskan advance. The retreat of the Cochrane is suggested at the hemlock minimum and hickory maximum (10-11); and its advance may be correlated

with the preceding rise in hemlock, reaching a maximum at the 15 ft. level. The previous decline in hemlock is suggestive of the Agassiz-Campbell retreat, and it is preceded by a slight increase which may be correlative with the advance of Agassiz-Campbell. The brief pine period may be correlated with the retreat of the Mankato.

The Mankato advance is suggested by the spruce maximum. The bottom sediments represent the period after the retreat of the Cary, which may have been accompanied by pronounced climatic amelioration indicated by the presence of oak. If these correlations are valid then this pollen profile supports MacClintock's belief that the bog has been developed on drift of Cary age (MacClintock, personal communication).

Present Vegetation–History

With the arrival of man, new influences were superimposed upon those previously controlling the vegetational pattern. Man's activities that affected vegetation were cutting the forests, carelessness with fire and cultivating the land. These activities resulted generally in more xeric conditions and therefore a retrogression in the vegetational development (Nichols 1913a).

The initial anthropeic influence upon the region began with the Indian, who depended mainly upon fruits and animals for his existence. He is known to have frequently set fires either accidentally or purposely to facilitate hunting (Little 1946, Vermeule, *et al* 1900). Later as white man entered the region he gradually cleared the areas suitable for agriculture. Later, industry grew up and this was accompanied by increasingly intensive harvesting of wood from the remaining forested areas. The dependence of industry upon forest resources reached its maximum during the middle 1800's. Large quantities of wood were required to supply iron furnaces scattered throughout northern New Jersey. During this period trees 20-25 years of age were cut and utilized as charcoal. Much wood was also used for many other purposes such as railroad ties, hoop poles, and domestic fuels. Around 1850 when anthracite blast furnaces were introduced, the utilization of forest resources began to decrease (Vermeule, *et al* 1900). However, by this time portions of the adjacent New Jersey Highlands were completely denuded of forest vegetation. Along with the intensive cutting were severe forest fires. During the special survey of forests from 1894-1899, Vermeule, *et al* (1900) pointed out that pitch pine as well as mixed coniferous and deciduous forests of the Kittatinny Mountains suffered considerably. Although a permanent organization to control fires was established as a result of this survey, frequent fires have since plagued the region. Present residents recall several large fires in more recent time, one or more of which burned over large areas along the major ridge within the park.

Today the effects of man's activities are evident everywhere: in the prevalence of sprout growth typical of cut-over oak woods, in the evidence of fires, and in the secondary succession patterns from old fields through gray birch to as yet unstabilized forest.

Vegetational Pattern

The dominant community is the chestnut oak with its characteristic ericaceous shrub layer. It forms a matrix in which all the other communities are found (Fig. 1, 20). It is relatively stable on most sites, but on some of the lower slopes it is yielding to the northern hardwoods. Since the disappearance of chestnut, natural replacement by oaks has followed. In Stokes State Forest, Korstian & Stickel (1927) noticed this trend.

The typical community of the rocky ridge top is the pitch pine-scrub oak community (Fig. 20, 21). Fires in the past have probably aided in perpetuating this community by stimulating sprout growth of scrub oak and furnishing favorable conditions for pine reproduction (Lutz 1934; Conard 1935; Little & Moore 1949). In fact, the vegetation resembles that found in parts of the Pine Barrens of southern New Jersey where frequent fires occur. With the exclusion of fire in the pitch pine-scrub oak community on the ridge top, the evidence indicates that both pines and arborescent oaks have great difficulty becoming established, and that shrubs may continue to dominate over considerable portions. Those pines

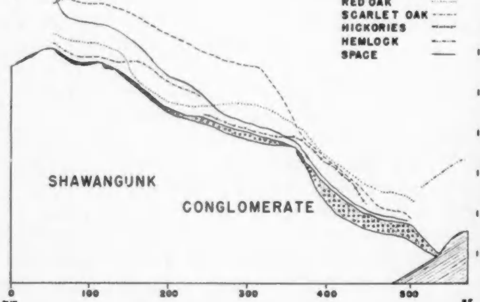

FIG. 20. Transect representing tree cover (Fig. 1, Transect B). The distance of each line representing the species above the topographic profile indicates the % of tree cover represented by the species at different points along the transect line. For example, on the ridge top (0-50) pitch pine contributes 88% of the total tree cover and open space in the tree canopy is at its greatest (70%). Other species are present but altogether contribute only 12% of the cover and are omitted here. On the slopes, chestnut oak contributes 62% cover, reaching a maximum of 71% (190), followed by an abrupt decrease to 25% on the lower slope (360-460). Chestnut oak on the lower slope is accompanied by approximately equal percentages of hickory and red oak. Scarlet oak is restricted primarily to the upper slopes (60-250). Numbers at the bottom refer to horizontal distance in meters and at right, refer to altitude in feet above mean sea level. Glacial drift overlying the geological formations is shown by stippled area with larger dots. Talus slopes are represented by small angular blocks. The Martinsburg shale is shown at right by oblique lines.

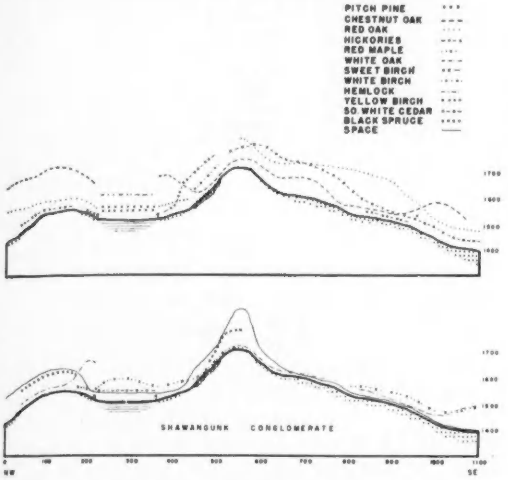

FIG. 21. Transect representing tree cover (Fig. 1, Transect A). See Figure 20 for guide in interpretation. Cedar Bog deposits are represented by parallel lines. Break in line across Bog (210-360) indicates that only a portion of bog was sampled. The letter (R) on either side of the bog indicates location of road.

present are primarily in the open early stages of primary succession. This community will probably continue to be represented as long as primary vegetational succession is still in the process of covering the bare rocky ledges, and as long as fires are allowed to sweep across the ridge.

In contrast, the pine-oak community as it occurs today, on the deeper soils derived from glacial drift, is an advanced successional stage approaching oak forest. Sporadic pines frequently tower above the arborescent oaks and the oaks are reproducing prolifically compared to the pine. Evidence of greater importance of pine in the past is indicated by rotten pine logs on the forest floor, by the occurrence of a podzol soil profile and by sporadic clumps of scrub oak. Very similar to this are late successional stages in the Pine Barrens of New Jersey (Buell & Cantlon 1950). In the absence of further pyric and anthropeic influences, the pine will form only a small part of the stands if present at all (Little & Moore 1949).

The white oak-hickory community occurs on the valley floors or in more mesic upland sites (Fig. 21, 22, 23). The presence of chestnut logs in some stands indicates that where hickory is present today both species, along with white oak once shared dominance. At present this community shows a successional trend toward the northern hardwoods. There is an increasing importance of the northern hardwoods in the smaller size classes. The mixed oak-hardwoods community in the same way is yielding to the northern hardwoods. The established northern hardwoods are at their maximum development in deep narrow valleys (Fig. 20, 23). Further aggressiveness by the more mesic species is evidenced by the young hemlock which is in the adjacent chestnut oak community.

Where land has been cultivated at some time in the recent past, gray birch is now common. Raup (1937) found the same situation in the Black Rock Forest of New York. Red cedar also occurs, but is not abundant. It is primarily restricted to the shale. In southern New England, Lutz (1928) and Raup (1940) describe both red cedar and gray birch in secondary succession. Bard (1952) found red cedar abundant and little gray birch on the Triassic shales of the Piedmont of New Jersey. The birch and cedar, which are relatively short lived, are replaced by an oak forest.

Since the recession of the ice sheet, primary succession has been continuously occurring on the scoured ledges of the ridge and in the glacial lakes. In fact, there is still bare rock to be covered and water to be filled in with vegetation. The earlier successional patterns were probably not unlike those operative today. The species concerned may well have been different; but the earlier the stage in the succession, presumably the more nearly the present vegetation resembles that of early post-glacial time. Plants that suggest this are lichens, mosses, and certain flowering plants such as *Deschampsia flexuosa* and *Potentilla tridentata*.

The process of primary succession is much the same for all rock surfaces although the ultimate vegetation which becomes established depends upon the exposure. On the ridge tops it leads to pitch pine-scrub oak or possibly to chestnut oak. In contrast, on the northwest slopes are northern species such as white pine, white birch, sweet birch, mountain ash, striped maple, and mountain maple associated with chestnut oak.

The early stages of bog succession at High Point, as in the rock succession, reflect the early boreal environment shown to have existed in the area by the pollen record. For example, species such as *Andromeda glaucophylla*, black spruce, tamarack and associated vegetation appear as relicts around which more southern species have become established as Transeau (1903) long ago pointed out. He believed that the presence of either a coniferous bog or broadleaved swamp vegetation depends upon the period in post-glacial time when a suitable habitat became available. Although both occupy the same kind of habitat today, the coniferous bog has been gradually losing out. Only where the conifer vegetation has been reasonably undisturbed has it persisted. Elsewhere, the swamp hardwoods have replaced it, and even without disturbance the succession appears to lead to a swamp hardwood forest with hemlock.

The occurrence of southern white cedar in Cedar Bog is of particular interest. Its invasion into the area may have occurred during the last xerothermic period or hickory maximum. Several investigators have found evidence to indicate that cedar may have been more important in the recent past (Bartlett 1909; Nichols 1913b; Raup 1937; Heusser 1949). Today it is decreasing and will ultimately give way to the more shade tolerant hemlock and red maple (Little 1950). The broadleaved swamp forest of more recent origin is relatively stable, with little

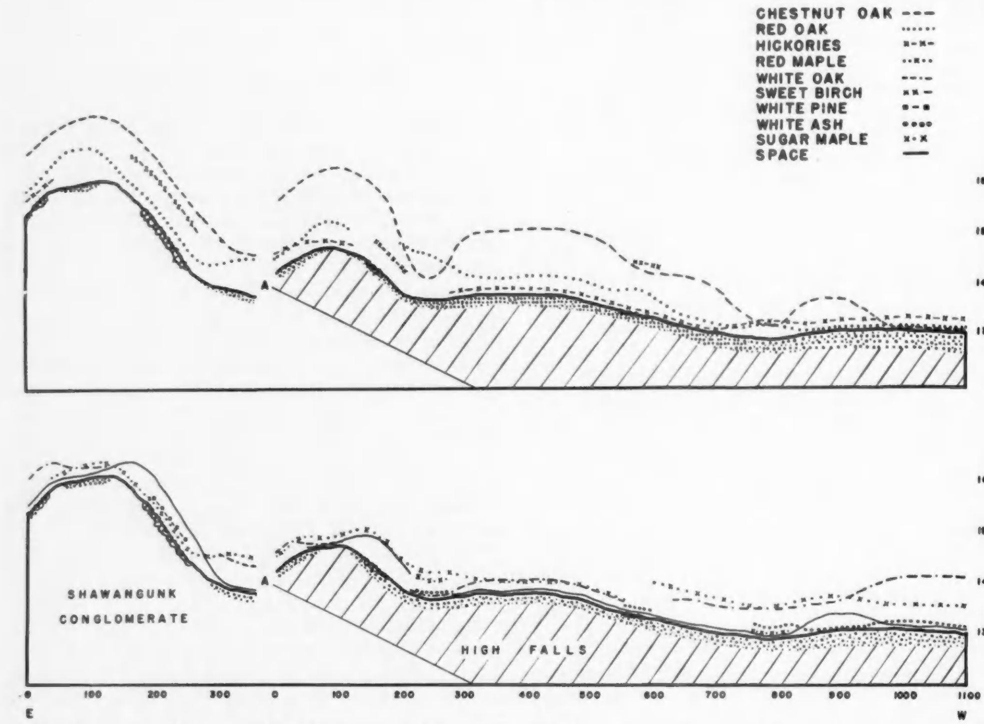

FIG. 22. Transect representing tree cover (Fig. 1, Transect C). See Figure 20 for sample explanation. Break in line A represents abandoned fields.

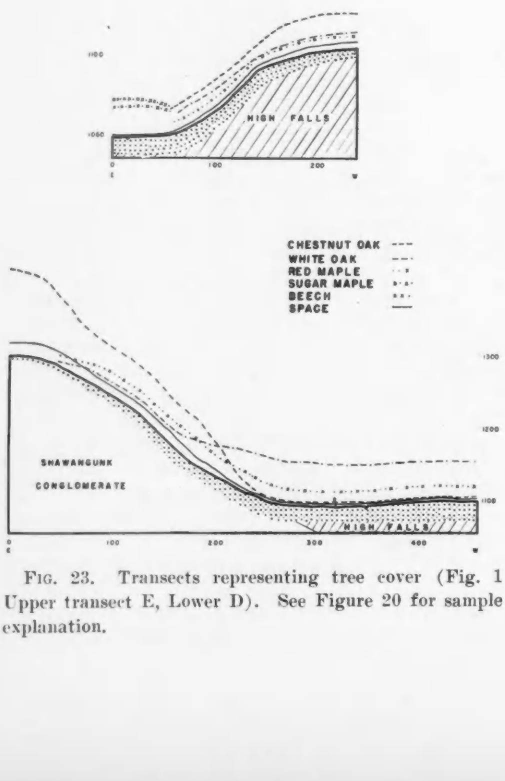

FIG. 23. Transects representing tree cover (Fig. 1 Upper transect E, Lower D). See Figure 20 for sample explanation.

evidence of change except where accumulation of soil has resulted in more mesic conditions. It is interesting to note that relict species whose range is more continuous either further north or south are found in both xerarch and hydrarch primary successions, which offer less competition than other habitats. Today the mosaic of vegetation in High Point State Park is composed of plant communities some of which are relatively stable, while others show successional tendencies. In recent time the activities of man have changed the forest from one which was more mesic, having a larger representation of northern hardwoods, to the more xeric types of today. The northern hardwoods are very restricted in their distribution; however they are expanding into the surrounding oak communities, a trend noted by Raup in the Black Rock Forest (Raup 1938). With protection rather than destruction more mesic conditions will develop, although the physiography and soils will always exert pronounced influences limiting the possible extent of mesophytic development.

SUMMARY

1. The post-glacial history of High Point State Park reveals an initial spruce-pine-fir-oak forest succeeded by a period of spruce-pine-fir and then a brief period of pine dominance. Finally there was a prolonged deciduous complex in which oak predominated. During the latter, two periods of hemlock

maximum with an intervening hickory maximum suggest climatic fluctuations from mesic, to xerothermic, with a return to mesic conditions.

2. Today a chestnut oak community with an associated ericaceous shrub layer is the continuous element of vegetation within the park. In other words, it forms a matrix in which occur all other communities.

3. The dispersed communities within this matrix and their typical sites are: the pitch pine-scrub oak on the rocky conglomerate ridge tops; the pine-oak on hills of the High Falls; the white oak-hickory on many of the valley floors, and some of the moist uplands; the mixed oak-hardwoods on the slopes of broad valleys between the hills; the northern hardwoods in the narrower valleys and deeper ravines; and of course, early successional stages of both primary and secondary succession.

4. Early stages of primary xerarch and hydrarch succession, initiated upon the disappearance of the Pleistocene ice, are continuing now, probably much the same as at their start. This is indicated by the part played by several boreal species.

5. The presence of certain disjunct southern species such as *Chamaecyparis thyoides* suggests relicts of the xerothermic period.

6. Primary hydrarch succession leads to a swamp hardwoods forest with hemlock. Disturbance has hastened the replacement of the northern conifers by this forest.

7. In secondary succession gray birch plays a dominant role. Red cedar, so important in southern New England and further south in New Jersey, is of minor importance. *Andropogon* species are unimportant except on the eastern fringe of the park where the shale outcrops.

8. The present vegetational pattern is a result of man's activities superimposed upon climatic, edaphic, and physiographic conditions. On most sites where they occur the chestnut oak, pitch pine-scrub oak, swamp hardwoods and northern hardwoods communities are relatively stable. The pine-oak, white oak-hickory, mixed oak-hardwoods communities show evidence of change. In the more xeric communities oak is replacing pine and in the more mesic communities the northern hardwoods are replacing the oaks and their associates.

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THE SAVANNA VEGETATION OF NORTHERN TROPICAL AMERICA

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INTRODUCTION

Until quite recently the writer of this paper was resident in the Caribbean Islands, a part of northern tropical America, and had frequent opportunities for studying the ecology of the region. This meant mainly dealing with forests, being employed as a forest officer, but in Trinidad there are some very typical though limited areas of tropical American natural grasslands and in studying these the writer so came to the conclusion that there was great need for a new approach to the baffling problems which this type of vegetation was found to present. Natural grasslands, commonly called savannas, cover vast areas of tropical America, but as this part of the world is still very much a "dark continent" scientifically we know very little of their composition or ecological relationships. The literature on the subject is relatively scanty and is dispersed in eight languages. Various different and opposing theories about the ecological relationships of the savannas are extant based often upon inadequate field data and (with the honorable exception of Rawitscher's recent work (1948)) with a total lack of experimental evidence. The writer formed the opinion that there was a need for a review in one monograph of existing information and theories and it is this object which the present study has before it. It begins with a review of existing definitions and theories about American savannas, which are discussed briefly. After this an attempt is made to set down what is known of the facts relating to savannas, region by region, and to examine the adequacy of current hypotheses in relation to them. Initially in this section the results, hitherto unpublished, of the writer's studies of the Trinidad savannas are set down in detail followed by observations drawn from travels in the West Indies and Venezuela. Available literature is drawn upon for information about other regions.

Finally there is a discussion of the whole subject in which an attempt is made to deal with some of the major questions which these grasslands present and which do not appear to have yet been adequately answered. The study is confined to savannas north of the Equator, partly for economy of space and partly because the writer has not had an opportunity to visit those lying to the southward. Passing references to

the literature only will be made where it is of particular interest to refer to savannas of the Brazilian plateau. Warming's (1892) work at Lagoa Santa is considered to be in conformity with the conclusions on the northern savannas, and more recently Waibel's (1948).

REVIEW OF LITERATURE

On their advent to tropical America, Europeans found vast stretches of land covered with more or less open grassland. These communities still exist much as they ever did, and appear to be quite stable. Such grasslands cover the greater part of the basin of the great river Orinoco, much of the South Brazilian highlands, some of the Guiana plateau and limited areas elsewhere in the Amazon, lowland Guiana, the Antilles and Central America. To them, the term "savanna" is commonly applied, though the terminology is confused. Any grassland in tropical America, with or without trees or shrubs, natural or man-made, is called a savanna today and in British Guiana it is even applied to areas of herbaceous swamp land from which grasses may be absent just as well as trees. The word is variously spelled—*sabana, savana, zabana* or *zavana* in Latin American countries; Bennett & Allison (1928) used *savana*, but *savannah* is the general English-language spelling. In English usage there seems no justification for the "h," but pronunciation seems to call for a double "n." Many dictionaries derive the word from the Spanish *sábana*, a sheet or blanket, the inference apparently being that the ground is as flat and bare as a sheet. The derivation ignores the difference in fall of the accent, very important in Spanish, and is clearly not the correct one. In a review of this matter (1936) Lanjouw showed by a series of quotations from early writers that savanna was an Amerindian word used in Haiti and Cuba for treeless plains. The first published mention of the word seems to have been made by Oviedo in 1535: "Este nombre *savana* se dice á la tierra que está sin arboledas, pero con mucha é alta hierva, ó baxa" (This name *savanna* is applied to land which is without trees but with much grass either tall or short.) The term savanna will be used here generally to designate all tropical American natural grasslands, but its exact application will be discussed more fully in the concluding section. In Brazil the word "campo" appears to be synonymous.

Ecological treatment of savanna began with Grisebach (1872) who attributed it to the alternation of wet and dry seasons. Grisebach envisaged a series of climatic zones. An equatorial region along the Amazon characterized by well-distributed rainfall and covered with rain forest was supposed to be bordered to north and south by drier regions with marked seasonal periodicity of rainfall in which grasslands became dominant.

The great ecologist, Warming, labored early in this field and his paper "Lagoa Santa" (1892) was not only the first special study to be directed to American savannas, but remains the finest to this day. Warming ascribed the savanna vegetation to a combination of special soil conditions and a dry, seasonal climate. His deep knowledge of field conditions made it clear to him both that there are curious and peculiar features about savanna as opposed to forest soils and that the climate by itself was adequate to support forest. The theory that the savanna had originated from destruction of forest by fire he excluded as "totally inadmissible."

Schimper (1903) was still obsessed by the climatic theory and wrote always of distinct woodland and grassland climates. A good grassland climate, he considered, should have frequent, even if weak, precipitations during the vegetative period and a moderate degree of heat then. Unfavorable to woodland is a dry, cool winter or a very long rainless season. The llanos of Venezuela, he said, have a climate "hostile to woodland" with a quite rainless dry season of five months and a continuously rainy wet season. The savanna country of South Brazil, on the other hand, he admitted to be less dry than the thorn bush and cactus country to the northeast of it, but explained this on the ground of the cool winter in the savannas.

In his later work (1909) Warming came out more fully in favor of a climatic theory and we find no mention of the soil beneath the savannas. "The vegetation is *xerophytic* in many places because of the dry season that lasts for months and . . . coincides with *winter*, during which often no rain falls and dew appears to be the sole atmospheric source of water. But the xerophily is also due to the dry continental climate in general." In Warming and Graebner (1918), we find the definition: "Tree-steppes (Savannas, Campos)—under this name we include those tropical grasslands with summer rain and winter drought, which are more or less covered with small trees. . . . The reasons for lack or scarcity of trees are partly geological, partly climatic." Hayek (1926) followed a climatic approach: "The typical form of the tropical grassland is the tree steppe or bush steppe. It is widespread in the dry parts of the tropics where the bulk of the rainfall falls during the vegetative period of grasses." Bews (1929), in a study of the world's grasslands based upon the historical evolution of the grasses which penetrated very deeply into the problem, regarded "tropical high-grass savannas" as derivatives from forest destroyed by fire. "Tropical bunch-grass savannas" however he regarded as essentially occupying areas where climatic factors are not suited to the maintenance of closed forest.

Other writers since have continued to adhere to the climatic theory, of whom we may mention Bouillenne (1930) and Myers (1936), authorities on the savannas of the interior Guiana plateau. Myers stated "the savannah vegetation is thus of climatic origin," associated with alternating wet and dry seasons. Later in the same work he qualified this categorical statement with the remark that "we are justified in regarding the present vegetation as a fire climax."

Nearly all writers have regarded fire as a second-

ary factor, on the assumption that a grassland or other low open vegetation was first present due to some climatic or edaphic cause and became liable to take fire easily, the fire later modifying the vegetation somewhat. Degradation of forest to savanna by felling and repeated burnings, the savanna thus being purely a fire climax, is popular with very few. Exceptions are Christoffel (in Aguerrevere & Ors 1939) who described the process of felling and burning practiced by aboriginal Indians of the Guiana plateau, and Rawitscher (1948) who arrived at this conclusion for savannas near São Paulo in Brazil.

As early as 1906 Pulle suggested that the savannas of Dutch Guiana were of edaphic origin and caused by leaching of the soil. For the same locality Ijzerman (1931) pointed out that the soil must be the cause since the savanna climate does not differ from that of surrounding forest country. He envisaged severe leaching, the rain water soaking into the soil of the savanna plateaus and down into the creeks. In due course the soil would become impoverished and "the result is an extremely barren soil on which nothing will grow." Lanjouw (1936) accepted the leaching theory of Pulle and Ijzerman, and added a rider on burning which he considered to have entered the picture as soon as the soil deterioration had sufficiently impoverished the forest, and further changed the character of the vegetation.

This view was reiterated by Pulle in 1938 and was taken up by Hardy (1945) who associated savannas with impoverished "Bleached Earth" soils which could only support a "poor sort of forest" due to their "inherently low fertility." In regions where there is a severe dry season this poor forest would be apt to be burned off and replaced by grassland or scrub.

Waibel (1948), studying the Planalto Central of Brazil, found "within a few square miles and under the same climatic conditions . . . semi-deciduous forests, cerradões transitional in character, campos cerrados with many low trees, the more open campos sujos, and the treeless campos limpos." These differences in vegetation, he concluded, depend mainly on differences in soil and ground-water conditions and, ultimately, the parent rock material. Waibel thus coupled geology with soil moisture. Jones (1930) had sought a purely geological relationship between savanna lands and sandstones and between forests and igneous rocks.

Bennett & Allison (1928) on the other hand, in their work in Cuba, ignored the geology wholly in favor of soil moisture relationships.

These authors wrote that "in Cuba the term savana, as applied to land, carries both a vegetative and a soil meaning. . . . As a rule the savana lands have at relatively shallow depths subsoils composed of material which affects the soil moisture conditions unfavorably." Generally, the savanna soils feature a permeable horizon overlying an impermeable subsoil. Sometimes this effect is due to the presence of rock which has not decayed deeply, sometimes to the superposition of a sand upon a clay horizon, sometimes to the occurrence of layers of pebbly ironstone concretions or massive ironstone sheeting. The result of these circumstances is drainage impedance, which is accentuated by low relief.

Charter (1941), working on the soils of British Honduras, a region physically very similar to parts of nearby Cuba, found the relationship of the savanna soils to be essentially similar with drainage impedance as the dominating factor. Charter further declared that the impedance was a natural development, with maturity, of alluvial soils and traced a series of soil types with increasingly impeded drainage covered with increasingly impoverished vegetation from forest to savanna, which he claimed to stand in a development relationship one to another.

Drainage impedance was also held to be the essential factor differentiating savanna from forest vegetation by Beard (1944) in a general treatment of the vegetation types of tropical America. Conditions too severe for tree growth result, it was suggested, from alternating periods of waterlogging and desiccation on lands with perched water-tables (generally on somewhat flat areas with impermeable subsoil of rock, claypan or ironpan).

To summarize, the following are the various theories in the field in connection with American savannas:

1. Climatic. Based on moisture deficiency.
   a. The savannas are due to alternating wet and dry seasons (Grisebach; Schimper; Hayek; Bews—for bunch-grass savanna; Bouillenne).
   b. The savannas are associated with a seasonal climate and special soil conditions which decrease available moisture (Warming).
   c. Rainfall periodicity is the root cause but the vegetation has subsequently been modified by fire (Myers).
2. Biotic. Based on man's activity.
   a. Savannas have resulted from destruction and burning of the forest by man (Christoffel, Bews—for high grass savannas, Rawitscher).
3. Pedological. Based on chemical deficiency in the soil.
   a. Profound leaching of the soil produced a poor, low forest which became liable to take fire readily and so was converted into savanna (Pulle, Ijzerman, Lanjouw, Hardy).
   b. Certain geological formations develop soils which can only carry savanna (Jones, Waibel).

Based on defective subsoil drainage.
   a. Savannas occur upon more or less flat areas with impeded soil drainage generally due to the presence of an impermeable layer in the soil (Bennett & Allison, Charter, Beard).

It will thus be seen that a very wide range of theory is in the field and that no one has yet brought forward a single and convincing viewpoint which has met with universal acceptance. The idea of a climatic relationship is the oldest, and theories which take account of the nature of the soil are more modern, particularly those which stress the drainage factor.

The more modern work has not, however, as yet generally ousted the older, principally, one supposes, because it has been of a specialized nature and limited to local areas. We still find that reputable authors continue to repeat and expound the traditional theories of the past without, apparently, having any knowledge of the evidence provided by more recent, more specialized work. A very good example of this occurs in the "Phytogeographic Sketch of Latin America" (Smith & Johnston 1945). The authors, botanists of international repute, speak of the bulk of savannas as being "definitely climatic rather than edaphic in origin."

Much of the confusion about the ecological relationships of savanna has evidently resulted from the fact that some areas suggest one explanation, some another. The Venezuelan llanos suggest a climatic origin, the savannas of Cuba and Surinam each suggest a different edaphic origin, while the Gran Sabana and the São Paulo area are both suggestive of the influence of fire.

DESCRIPTIVE MATTER

THE ORINOCO PLAINS

The basin of the great river Orinoco contains a considerable area of savannas which stretch virtually unbroken from the foothills of the Andes and Coastal Cordillera in the north and west, across the river to the forested broken country descending from the Guiana shield. To the north and west of the river the savannas cover extensive flat plains formed by sediments of Quaternary age and at a very low elevation above sea level. These are the well-known "llanos." To the south and east of the river the savannas cover low, undulating country of small relief underlain by ancient rocks and representing a reduced and eroded portion of the Guiana shield. The latter region is described below in the section on lowland Guiana. The island of Trinidad, lying off the north-east Venezuelan coast, is structurally a part of Venezuela and has only become separated from the mainland in geologically recent time. At no very distant date the Orinoco entered the sea further to the eastward and the Gulf of Paria was an extensive plain of dry land uniting the flat southern portion of Trinidad with the Venezuelan plains north of the Orinoco. Savannas in Trinidad may, therefore, logically be grouped with those of the llanos for purposes of study. The writer has spent many years in the island of Trinidad and has had abundant opportunity to examine the savannas which occur there. A journey was made in February 1945 across the llanos of Venezuela along the main road from Ciudad Bolívar to Caracas via El Tigre, Pariaguan, Santa Maria de Ipire, Valle de la Pascua and El Sombrero.

THE ISLAND OF TRINIDAD

In the days of Christopher Columbus, the West Indian island of Trinidad was almost entirely covered with forest. Certain low-lying, inundated areas bore then as they do today a herbaceous vegetation of giant sedges or semi-woody plants such as *Montrichardia aborescens*. Around the coasts a few clearings had been made by scattered communities of Arawaks for planting their gardens. The overwhelmingly greater portion, however, of Trinidad must have supported various types of forest as the climax vegetation.

Settlement of Trinidad by the Spaniards did not take place on a large scale. In 1797 a British force conquered the island, which has since remained under the British Crown. After the conquest a survey of the colony was undertaken by Capt. F. Mallet of the Royal Engineers and a map published in 1802, a copy of which is still preserved at the Crown Lands Office in Port of Spain. This map, on a scale of about 1:100,000, showed the existing estates and indicated the crops they were producing: such settled lands amounted then to about 10% of the total land area and were situated around the coasts. Remaining lands, where considered suitable, were shown marked out for settlement and indications were given of the main features of the colony, such as "mountains of the north coast, inaccessible and generally covered with incorruptible woods" (*sic*). In the interior of the country in several places, buried often deep in forest, he indicated a number of "natural savannas." These still exist to this day. None has been utilized for agriculture, though in some cases cultivation has reached their borders. Several of the savannas remain surrounded by more or less undisturbed forest. At the present time some additional areas of grassland exist in the island, not shown by Mallet and differing from those he recognized in important respects. Mallet's "natural savannas" are all in the lowlands and are of closely similar floristic composition. Of the others, one is floristically similar (in part) to Mallet's but covers mountainous terrain, and the remainder lie in the lowlands but are floristically dissimilar. In summary the grasslands fall into three groups:

1. "Natural Savannas" (lowlands)
   a. Erin and St. John savannas
   b. Piarco, Mausica and O'Meara savannas
   c. Aripo savannas
2. Other savannas (mountain)
   a. St. Joseph savanna
3. Other savannas (lowlands)
   a. Cocorite savannas of the Northern Plain.

The above list does not include pastures and other grasslands deliberately created by man, but embraces only areas which have become covered with grass in response to natural conditions or to man's unintentional influence.

Reference to these savannas is found in Marshall (1934, p. 39-40) and in Myers (1933, pp. 344 *et seq.*). The writer has also had access to an unpublished thesis on "The grasses of Trinidad" by J. H. Hinds, 1940, at the Imperial College of Tropical Agriculture.

THE ERIN AND ST. JOHN SAVANNAS

The Erin and St. John savannas are the two savannas, or rather groups of savannas, in the south of the island and may be described together as they are very closely similar. The Erin savanna—it is generally referred to in the singular—is a group of small stretches of grassland varying in size from less than one acre to one hundred acres lying immediately east and west of Buenos Ayres village on the Erin—Cap de Ville Road. The total area of the grasslands is about 240 acres, and they are shown mapped in Figure 1. On Mallet's map the Erin savanna is not accurately placed, but is shown surrounded by forest as there was very little settlement in the vicinity at that time. One or two small parcels of savanna have since been included in alienated land near Buenos Ayres village but the bulk remains as before deep in forest. The St. John savanna occupies about 20 acres on the St. John estate near Oropouche village about eight miles south-west of San Fernando. On Mallet's map it is marked as a "natural savanna" on the estate which was then cultivated in sugar canes. The savanna today is used for rough grazing and is surrounded by degraded secondary forest.

The savannas are generally flat and occupy plateau sites, though in places the grassland covers slopes descending round the plateau edges. The Erin savanna lies along the crest of a watershed and the St. John savanna caps a Pleistocene terrace deposit. There are strong indications that these savannas occupy the remnants of an ancient land surface, a peneplain which in recent geological time has been uplifted and which is still being very actively dissected. Forest lands surrounding the savannas occupy sharply undulating topography.

The savanna soils are of a very special character. The geological parent material underlying the savannas does not differ from that beneath the surrounding forest but the soils developed on the two sites are dissimilar. In the surrounding country there are occasional outcrops of sandy beds and porcellanites which yield sandy soils, but in the main the formation is a clay-shale which yields on the forest sites an exceedingly stiff clay soil, sticky and impermeable in the wet season, hard and deeply cracked in the dry season. From the surface down to about 12 in., the clay is dark brown and crumbly with good penetration of small roots and organic matter. Below this depth it merges gradually into a greyish-brown clay with red mottlings into which roots still penetrate, and below some 6 ft. into a bluish grey clay with red and tawny mottlings and some iron concretions. Typical profiles of forest and savanna soils are pictured in Figure 2 by permission of Prof. F. Hardy from notes taken by C. Swabey and C. G. Akhurst in 1930 and the relevant laboratory data are given in Table 1. On the flatter, more definitely

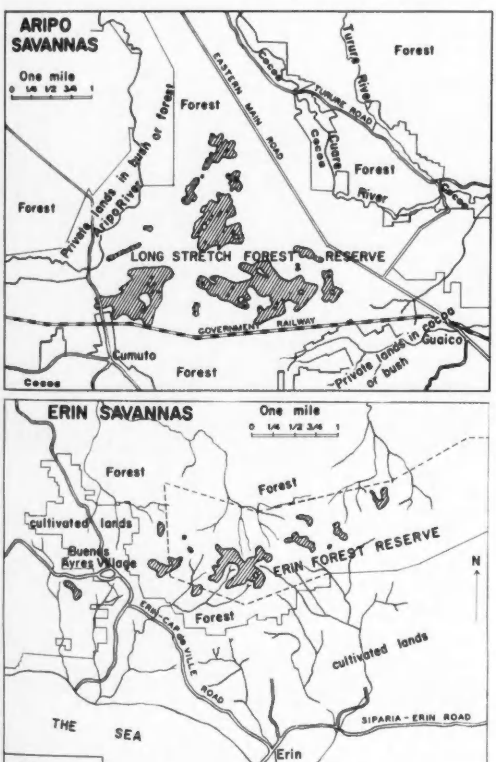

FIG. 1. Large scale maps of the Aripo savannas (top) and Erin savannas (bottom), from aerial survey.

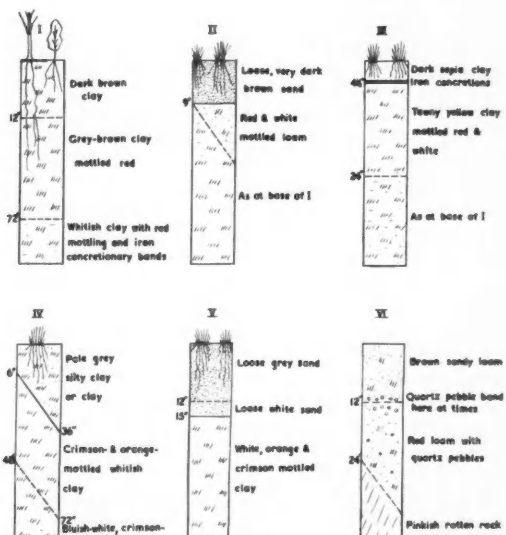

FIG. 2. Typical profiles of savanna and forest soils in Trinidad. I. Forest soil. II. Erin savanna soil (Beard). III. Savanna soil at the Erin Savanna (after Swabey & Akhurst). IV. Long stretch silty clay of Aripo savanna area. V. Piarco light sand of Piarco, Mausica and O'Meara savanna areas. VI. Maracas light sand of the Northern Range (after E. M. Chenery).

TABLE 1. Laboratory Data for Soils at the Erin Savanna.†

Depth ins.		Index of Texture	Reaction: Norm. pH	Reaction: Exch. pH	Org. Matter* %	N %	C/N Ratio*	Av. Nutr. mhos	Rate of Soln. x 10^{-6}	Av. P^2O^5 p.p.m.
	GRASS TYPE. (grass, with Curatella and Byrsonima)									
½	Black, humic, roots	35	4.4	3.8	6.66	0.24	15.9	98	8	13
2	Dark, sepia humic	34	4.6	3.8	6.12	0.28	12.5	38	5	19
4½	Sepia, iron concretions	34	4.6	3.9	5.56	0.21	15.2	43	5	9
8	Tawny, mottled red	34	4.5	3.9	3.12	0.16	11.3	28	12	6
14	White, tawny, red mottling	40	4.6	3.9	1.35	0.08	10.4	22	9	4
24	Grey-white, red mottling	51	4.6	3.8	0.48	0.06	4.4	19	4	5
36	Ditto	51	4.5	3.8	–	–	–	27	6	5
48	Ditto. Iron concretions	46	4.5	3.7	–	–	–	31	21	5
60	Ditto Ditto	38	4.6	3.7	–	–	–	17	6	6
84	Ditto Ditto	43	4.5	3.6	–	–	–	28	13	5
	FOREST TYPE. (Carapa, Eschweilera, Maximiliana, etc.)									
½	Dark sepia humic	36	4.6	3.8	7.31	0.26	16.3	68	11	15
2	Ditto	31	4.6	3.8	6.37	0.26	14.3	53	12	39
4	Ditto	30	4.6	3.9	5.97	0.23	15.1	52	8	19
6	Paler sepia	28	4.8	3.9	4.99	0.19	15.3	34	14	18
9	Ditto	25	4.5	3.9	3.72	0.14	15.9	27	6	14
13	Yellow sepia	27	4.5	3.9	2.09	0.10	11.9	23	6	10
20	Grey sepia	37	4.4	3.9	1.21	0.10	7.3	23	11	8
36	Grey, red splotches	36	4.5	3.9	–	–	–	20	4	6
48	Ditto	31	4.4	3.8	–	–	–	26	5	8
63	Ditto	27	4.4	3.8	–	–	–	21	2	7
72	Blue-grey, red & tawny mottling	43	4.5	3.7	–	–	–	47	1	10

*Corrected.

†Published by permission of Professor F. Hardy from records of samples taken by C. Swabey and C. G. Akhurst in 1930 and analysed at the Imperial College of Tropical Agriculture.

plateau-like portions of the savanna the clay is found to be overlain by a horizon of loose, dark sand (profile II, Fig. 2), but on sloping ground this sand capping is absent (profile III). In the former case the sand is some 9 to 12 in. deep, very dark colored and incoherent, full of grass roots. A sudden break occurs at the base of this horizon and there is a change to tawny, red and white mottled loam or whitish clay with red mottlings. Iron concretions may be present. Grass roots but not tree or shrub roots penetrate this layer which is extremely compact. The soil of sloping ground is typically at the surface an almost black clay, hard and very compact, full of grass roots. Below 4 or 5 in. scattered iron concretions appear and the upper horizon gradually merges into a tawny yellow clay mottled red and white. This in turn merges below some 2 ft. into a whitish clay with brilliant red mottlings and abundant iron concretions which often occur in bands. In many places on sloping parts of the savanna, often appearing as an outcrop just below a plateau rim, there are abundant ironstone boulders of all sizes, but there were never any ironstone boulders or slabs at depth in any soil profile examined. The clay topsoil is highly compact and impermeable and during a heavy rainstorm the water moves off the surface in a sheet. Apparently there is little absorption of water into the soil or erosion of the surface by this sheet runoff. The ground surface is regular on slopes but on plateau sites is often "hogwallowed," that is, shows a curious irregular configuration of hummock and depression (Fig. 3).

FIG. 3. Area of low bush adjoining the Piarco savanna after a fire, showing "hogwallow structure" of the ground surface, an irregular configuration of hummocks and channels.

The savannas are of "tall bunch-grass" type with scattered shrubs (Fig. 4). A photograph taken after a fire (Fig. 5) shows the arrangement of the grasses into scattered clumps with bare soil between. The grasses grow normally to a height of about 18 in. During the dry season which lasts generally from January to May and during which there is usually between ½ and 2½ in. of rain each month, the grasses dry up and die down somewhat. During this period the savanna may be swept by fire, presumably set by human agency. On the average a fire occurs probably once every 4 or 5 years. At the onset

FIG. 4. Typical physiognomy of the neotropical savanna: the Mausica Savanna, Trinidad.

FIG. 5. Savanna shortly after a fire, showing the disposition of grass clumps and the actual extent of soil cover. The machete and notebook give the scale. In rear are two small Byrsonima bushes with scorched leaves. Note that the fire was not fierce enough to consume the grasses to the root.

of the rainy season in May or June the grasses, whether burnt or not, sprout vigorously and proceed to flower, the spikes reaching about 5 ft. high. After this general flowering, individual grass clumps can be found flowering sporadically for the remainder of the wet season. During the rainy period from 5 to 24 in. of rain may fall each month. Total annual precipitation amounts to about 60 in. on the average. The dominant grass is *Axonopus anceps* (Mez) Hitchc. Associates are *Setaria geniculata* (Lam.) Beauv., *Paspalum fasciculatum* Willd. *Sporobolus* sp., *Andropogon bicornis* L. and *Leptocoryphium lanatum* Nees. In sandy places *Trachypogon ligularis* Nees is common as is a small sedge with delicate feathery leaves, *Bulbostylis junciformis* (HBK.) Lindman. In many places, particularly near the borders of the savanna, "razor grass" (sedge) *Scleria bracteata* Cav. is abundant. Many herbs are found among the grasses, and one may mention *Sipanea pratensis* Aubl., *Crotalaria pterocaula* Desv. and *C. stipularia* Desv., *Elephantopus angustifolius Sw.*, *Sida linifolia* Cav., *Rolandra fruticosa* Rottb., *Desmodium barbatum* Benth. & Oerst., *Buettneria scabra* L., *Martiusia laurifolia* (Poir.) *Britton*, *Curculigo scorzoneraefolia* (Lam.) Benth., *Eriosema* spp., *Hyptis* spp., and *Polygala* spp. Small gnarled trees up to 10 ft. high occur scattered freely about the savanna and with the exception of some little melastomes (conspicuously *Miconia macrophyrsa* Benth.) which do not often exceed 2 or 3 ft. in height, belong to *Byrsonima crassifolia* HBK. and *Curatella americana* L. Of these two Byrsonima is the commoner, the proportion being about four to one, but Curatella grows the larger. The peculiar gnarled form of these trees may be seen in the photographs. On the average they are scattered about 20 ft. apart. Leaves are coriaceous and large (4" x 2" in Byrsonima, 8" x 5" in Curatella) and the bark is thick, giving resistance

to grass fires. Very occasionally, usually in hollows, a palm, *Mauritia setigera* Gr. & Wendl., is found.

In sandy places small mound-nests of two species of termite are occasionally found on the ground, frequently based on an old stump or rootstock. These nests are seldom more than 12 in. high and narrow in proportion, and they are built of a brittle, blackish material exactly like the nests constructed by forest termites in trees. The late Prof. A. M. Adamson examined these mounds and their inhabitants with the writer and found two forms of Nasutitermes, one of which appeared to be morphologically indistinguishable from *N. ephratae*—a forest termite—and the other to be a new species. Prof. Adamson believed that the former will prove to be distinct from *N. ephratae* so that both these termites will belong to a distinct savanna fauna.

Very rarely do the grass fires penetrate the surrounding forest, they run up to its borders and there stop. Much of the forest in Trinidad has, however, been burnt by human carelessness in recent years during severe droughts, and the whole of the forest in the Erin district has been badly burnt out. In the vicinity of the savanna the fire may have run over from the grassland or may just as likely have originated on cultivated lands nearby. Formerly the forest surrounding the savanna was an evergreen seasonal forest of the *Carapa guianensis*—*Eschweilera subglandulosa* association, a dense "moist" forest 120 ft. high. It is today somewhat ruinate and the principal components are *Pentaclethra macroloba* (Willd.) Ktze, *Protium guianense* (Aubl.) March, *Clathrotropis brachypetala* (Tul.) Kleinh., *Cecropia peltata* L., *Inga* spp., species of *Lauraceae* and *Melastomaceae, Vismia* spp., *Guazuma ulmifolia* Lam., *Spondias mombin* L., *Byrsonima spicata* (Cav.) Rich., *Laetia procera* (Poepp. & Endl.) Eichl., *Pouteria minutiflora* (Britt.) Sandwith and the palms *Maximiliana elegans* Karst. and *Astrocaryum aureum* Gr. & Wendl.

Transition from the savanna to forest is very abrupt. The actual transition zone is only a few feet wide and is marked by an abundance of melastomes—notably *Miconia ciliata* (Rich.) DC. and *M. minutiflora* (Bonpl.) DC.—and razor grass (Scleria) and the sporadic occurrence of the grugru palm, *Acrocomia ierensis* L. H. Bailey.

Almost the whole of the savanna flora is peculiar to such grasslands and is not found in other types of vegetation. The Acromia palm has become common in Trinidad in areas subject to shifting cultivation but is unknown elsewhere in natural forest. As *A. ierensis* is endemic to Trinidad, its focus of origin must be in the fringes of the Erin Savanna. It appears probable that burning is essential to the germination of the thick-walled Acrocomia seed and hence its appearance in the much burned bush in and around peasants' gardens, and on the fringes of the savanna where soil conditions are substantially those of the forest but where the fire sometimes passes. The occurrence of this endemic palm, restricted as it is to this place, would seem to indicate that the savannas are very ancient and that in terms of human time they are practically stationary, neither expanding nor contracting.

Chemical analysis of savanna and forest soils derived from the same parent material as shown in Table 1 does not disclose any significant differences. Evidently the important differences must lie in the physical character of the soil and concern moisture relationships. This is in any case what one would expect, since it is a circumstance that has been repeatedly proved in studies of natural vegetation in the tropics.

Studies were made of the root-systems of savanna plants. The typically fine fibrous roots of the grasses were found to ramify abundantly in all directions in the upper, sandy soil horizon and there was also some penetration of the underlying red mottled clay zone. Root systems of the Byrsonima and Curatella trees were essentially similar to one another and a noticeable feature was the absolute lack of any penetration of the red mottled clay zone. In the upper sandy layer the root stock typically sent off a whorl of roots about ½ in. thick which meandered for long distances through the sand horizon without much branching and without any small lateral roots with root hairs. A typical root of this type was traced from a parent 6 ft. high Curatella tree for 27 ft. before it gave off a single branch. These root systems are feeble indeed, so much so that the trees are often blown down by the wind. The clay zone of the savanna soil is so compact that it may present a physical obstacle to the penetration of tree roots, but a physiological reason seems more probable. Clay soils of the forests are crumb-structured at the surface and are of a shrinking type so that the lower layers are to some extent opened and aerated in the dry season. Tree roots are able to penetrate and are not entirely deprived of air. On the other hand the brilliant mottling of the clay zone under the savanna indicates that it is largely sealed off from any aeration. In effect, a clay-pan is present. Water collects in the sand horizon over the clay in flat places and forms a swamp in the wet season. In the dry season the sand horizon dries out completely and the trees, having no deep roots, are subjected to severe desiccation.

THE PIARCO, MAUSICA AND O'MEARA SAVANNAS

The savannas of Piarco, Mausica and O'Meara are a group lying on the western part of the northern plain at the foot of the Northern Range. The topography of the whole area is very even and consists of a series of flat terraces deposited during Pleistocene time from erosion of the mountains to the northward. More recently the rivers have cut down their beds below the terraces, leaving these as dissected plateaus. The savannas occupy the central portions of certain of these terrace-plateaus. In Mallet's day they were more or less surrounded by forest, but since that time abortive attempts have been made at cultivation in the immediate vicinity and the savannas today are surrounded by an ex-

ceedingly poor secondary growth. Formerly this was evidently of the same Carapa-Eschweilera type as surrounded the Erin savanna, but it is now a tangle of low trees and lianes about 50 ft. high and with a very high proportion of the cocorite palm, *Maximiliana elegans* Karst. This bush merges gradually into the savannas and there is no sharp transition. Both forest and savanna here are very frequently burnt in the dry season, the fire generally escaping from a peasant's garden or a cane-field.

There is considerable similarity between forest and savanna soils on these terraces. A typical profile is shown in Fig. 3 (V). The upper layer of the soil down to some 12 in. consists of a dark to whitish-grey, loose, fine sand merging into a narrow band of loose white sand. Below this an abrupt change takes place to a stiff and compact white, orange and crimson mottled clay. The ground surface is deeply "hogwallowed" both on the savanna and in the flatter parts of the forest.

Floristically these savannas resemble the Erin savanna very closely. The tops of hummocks are occupied by *Paspalum pulchellum* HBK., co-dominant with *Leptocoryphium lanatum*. *Paspalum serpentinum* Hochst. is frequent, and *Thrasya paspaloides* HBK. and *T. robusta* Hitchc. & Chase are rarer. *Trachypogon ligularis* is present under trees. In the hogwallow channels and depressions one finds *Leersia hexandra* Sw., *Panicum stenodes* Gr. and *P. parvifolium* Lam., and *Sacciolepis myuros* Chase., *Andropogon leucostachyus* HBK., *A. selloanus* (Hack.) Hack. and *Paspalum pilosum* Roth., are sporadic throughout. Round the edges of the savanna *Arundinella confinis* Hitchc. & Chase and *Imperata brasiliensis* Trin., appear. The bladderwort and sundew, *Drosera capillaris* Poir., and *Utricularia* spp., are found in depressions.

The list of herbs present is substantially the same as for the Erin savanna and the same *Byrsonima crassifolia* and *Curatella americana* form the tree crop. Many little melastomes are also present, notably *Miconia albicans* (Sw.) Triana, *M. macrothyrsa* Benth., *M. stenostachya* DC., and *M. savannarum* Williams (an endemic). The palm Mauritia does not occur here.

In the very centre of the Piarco savanna where the ground is flattest and worst drained there are patches where shrub and tree growth ceases, the only woody plant being *Byrsonima verbascifolia* (L) Rich., which is a ground plant (Fig. 6.). Grasses here are shorter and *Paspalum densum* becomes common. The little sedge, Bulbostylis, becomes abundant. This is the only place in Trinidad where *B. verbascifolia* is found and its occurrence along with the endemic *Miconia savannarum* and several endemic herbs would indicate that at least the central portion of the Piarco savanna is of great antiquity.

Mounds of the same two termites described from the Erin Savanna are quite common on these savannas.

The former borderlines between these savannas and the forest have been destroyed by intensive burning.

FIG. 6. Centre of the Piarco Savanna. In the foreground, waterlogged area with sedge and *Byrsonima verbascifolia;* in rear, trees of *B. crassifolia* and grass.

Towards the edges Imperata and Arundinella become abundant. Maximiliana palms appear among the savanna shrubs and gradually increase in number until the poor forest is entered.

THE ARIPO SAVANNAS

The savannas of Aripo are a group of grasslands of variable size totalling some 680 acres, enclosed within the forest of the Long Stretch Reserve on the east-central portion of the northern plain. Mallet does not show these. Possibly in his day they were too remote to be noticed. There is an account of them in Charles Kingsley's "At Last" (1871). The savannas are found in the middle of a single large old alluvial terrace lying between the Aripo and Cuare rivers and forming the central watershed of the northern plain. The Aripo river joins the Caroni and flows westward, the Cuare flows east to the Oropouche. Topography is very flat across the whole terrace and some of the savannas were found to occupy slight depressions when some level traverses were run in 1941. The terrace land here is well recognized to have absolutely no agricultural value so that the forest has never been cleared away and is now a Forest Reserve. The rainfall here is much higher than further west, averaging about 110 in. annually. The dry season is shorter, only three months of the year, on the average, having under 4" of rain but over 2". As a result, neither the forest nor the savannas are known to have been burnt in recent times.

There is only a single soil type beneath the savannas and their surrounding forest Fig. 2 (V), consisting of an exceedingly stiff, very fine clay containing almost no sand. The surface horizon down to between 6 and 36 in., is a pale grey silty clay or clay and merges below into a brilliantly crimson and orange mottled whitish clay. The parent material is a bluish white, crimson-mottled clay. This clay is kaolinitic and exceedingly compact and impermeable. There seems to be almost no downward percolation and the soil remains remarkably dry at a depth of several feet even when the surface is waterlogged. In the northern part of the terrace, forest of substantially the same type as that surrounding the savanna is underlain by a soil consisting of about 36 in. of

loose grey sand overlying an iron-cemented gravel which creates an impermeable pan.

In the forest the ground surface is very markedly hogwallowed and this phenomenon is still present to a less pronounced degree on the savanna.

By strictest definition the Aripo savannas should be considered properly as herbaceous swamp since sedges predominate over grasses. On general characters of physiognomy and habitat it is preferable, however, to class them as savannas. This is a typical savanna site in point of soil and topography but the high rainfall so accentuates and prolongs waterlogging that the habitat begins to approach that of herbaceous swamp where the site is more or less deeply inundated for most of the year.

The dominant sedge is *Lagenocarpus guianensis* Nees., and associates include *Rhynchospora longibracteata* Boeckl., and *Bulbostylis junciformis* (HBK.) Lindman. Grasses are not very abundant but one finds *Paspalum pulchellum, Thrasya paspaloides,* and *Leersia hexandra.* The Lagenocarpus grows to about eighteen inches high. Most of the other sedges and grasses only reach about half this height and the general appearance is of shorter growth than the true grass savannas. *Drosera capillaris,* and *Utricularia* spp., are present and a number of small ferns. A sphagnum-like moss covers the open ground between sedge stems and grasses. Rather a prominent feature of this area are the several beautiful terrestrial orchids, of which the commonest are the white-flowered *Otostylis brachystalix* (Reichb. f.) Schltr., and the red flowered *Epistephium parviflorum* Lindl. During the dry season the soil often dries hard and cracks deeply. At the beginning of the rains the herbaceous plants sprout vigorously and flower but activity dies away at the height of rains when the ground is covered with standing water. At such times and in drought also the Aripo savannas exhibit a somewhat sere and drab-brown appearance. The savannas are dotted with small shrubs about three feet high and ten to twenty feet apart of *Chrysobalanus pellocarpus* Mey., *Miconia ciliata* and *Ilex arimensis* (Loes.) Britt. *Byrsonima crassifolia* is occasional and prefers any places where the ground is slightly raised. Curatella is absent. Occasional clumps of the endemic spiny palm *Bactris savannarum* Britton may attain 6 ft. high. Mounds of the same termite are found but are not as common as on the Piarco group of savannas.

The flora of this area is much the richest of any of the savannas and contains a greater proportion of endemic plants. These features may be attributable to the higher rainfall both directly in point of moisture and indirectly in point of the absence of burning.

Transition to forest is abrupt (Fig. 7). Along a sharply marked line one enters a dense thicket about 20 ft. high of small and rather gnarled trees with very long branches, of which the principal are *Chrysobalanus pellocarpus* Mey., *Ilex arimensis, Pouteria* sp., *Clusia nemorosa* Mey., and *C. palmicida* Rich., *Symphonia globulifera* L.f. and several Melastomaceae. Palms of *Mauritia setigera* Gr. & Wendl., stand out above the pole thicket. In the ground layer one finds *Bactris savannarum,* a Gleichenia fern, a Eupatorium and a cutting Scleria. Besides fringing the savannas this type of vegetation is found as "islands" in their midst. Away from the savanna the woody growth increases rapidly in height and at a distance of 20 yards from the edge has merged into high forest. This forest is not the same as that surrounding the savannas previously described. It is a somewhat specialized type, and belongs to the marsh forest of Beard (1944), the lower type of fringing thicket described above being his palm-marsh. The marsh forest is two-storied. Canopy is formed from 10 to 30 ft. from the ground by a lower story above which stand out occasional trees reaching about 80 ft. high in places. The bulk of the lower story is composed of the palms *Jessenia oligocarpa* Gr. & Wendl. and *Manicaria saccifera* Gaertn., with species of *Euterpe* and *Oenocarpus.* Conspicuous among large trees are *Calophyllum lucidum* Benth., *Pouteria* sp., *Parinari campestris* Aubl., and *Terminalia amazonia* (J. F. Gmel.) Exell. Tree roots seem to be confined to the upper layers of the soil but palm roots penetrate deeply into the clay pan.

FIG. 7. The Aripo Savanna and its sharp boundary fringed with Chrysobalanus and Mauritia. The savanna itself is a low growth of sedge with a few tiny shrubs.

THE ST. JOSEPH SAVANNA

The St. Joseph savanna is situated on the slopes of the Northern Range above St. Joseph and St. Augustine, between altitudes of 500 and 1500 ft. The slope is southerly and steep, the average slope being about 2 in 5. The mountains are composed of schists of lower Cretaceous age in which there is a variable proportion of quartzite. At this particular place the rock appears to be exceptionally highly quartzitic, the mineral occurring in particles of all sizes from small grains to large boulders.

In the Northern Range as a whole and in forest areas hereabout the soil developed over schist has a typical profile as shown in Figure 2. (VI). On the savanna there is, properly speaking, no soil but only bedrock and the savanna is clearly very severely eroded. The bunch grasses offer no protection against surface erosion and gullies form in between

the clumps. A little reddish earth covers the surface for the most part but the parent rock shows in many places and quartz boulders are abundant everywhere. The effect of erosion, by bringing bedrock close to the surface, is to create the effect of a pan, the rock being substantially impermeable to moisture and mechanically resistant to root penetration. External drainage of the profile is very good owing to the steepness of the slope.

The history of this savanna is obscure. It is not shown on Mallet's map but there is a vague record by an early Spaniard who was taken by Indians to an open place above St. Joseph whence he could view all of Trinidad. The present boundaries of the savanna are probably by no means stationary. Shifting cultivation has been practiced for a great many years on these mountain sides and the original forest, whose nature can no longer be decided, has been reduced to a secondary growth up to 50 ft. in height containing principally *Tabebuia serratifolia* (Vahl.) Nichols, *Machaerium robinifolium* (DC.) Vogel, *Protium guianense* (Aubl.) March and *P. insigne* Engl., *Oliganthes condensata* Schulz., *Apeiba schomburgkii Szyszyl.*, species of *Pisonia, Coccoloba* and *Croton,* and numerous Myrtaceae. Transition to grassland is gradual and usually takes place through a zone of low, burnt bush thick with vines and containing a few unhealthy looking Aerocomia palms.

There are two types of savanna here: the one, which may be called the Byrsonima-Curatella type (Fig. 8), resembling the lowland savannas of Trinidad and the other, the Myrcia-Roupala type (Fig. 9), which is *sui generis.* In only one place are the

FIG. 8. Section of the St. Joseph mountain savanna with Curatella and Byrsonima trees.

types contiguous and there the transition is abrupt and occurs along the crest of a ridge. The dominant grass *Trachypogon ligularis* is the same in both. On the Byrsonima-Curatella savanna it is associated with *Arundinella confinis* Hitchc. & Chase, *Thrasya paspaloides* HBK. and *T. robusta* Hitchc. & Chase. A Scleria "razor grass" is occasional. Shrubs of *Byrsonima crassifolia* and *Curatella americana* cause a very strong resemblance of this type to the lowland savanna, though the shrubs here are frequently more stunted and more scattered. On the Myrcia-Roupala savanna Trachypogon is less abundant and is almost co-dominant with the Scleria. Grass cover is much less dense, bare soil being rather generally visible, and the shrubs grow relatively thickly almost touching one another. The most abundant shrub is the microphyllous *Myrcia stenocarpa* Kr. & Urb., associated with *Roupala montana* Aubl. Others noted include *Rapanea guianensis* Aubl., *Curatella americana* L., *Pisonia eggersiana* Heimerl., *Inga venosa* Gr., and several melastomes, but all these are much rarer than Myrcia and Roupala. *Byrsonima crassifolia* seems to be absent or very rare in this type.

FIG. 9. Section of the St. Joseph mountain savanna with almost closed scrub of Myrcia, Roupala, etc.

Very occasionally a shrub of Myrcia, Roupala, etc., can be found on the Byrsonima-Curatella savanna. The characteristic gnarled growth of the shrubs on the latter is not adopted by *Myrcia stenocarpa* and its associates, which are of low growth, never over ten feet high but of erect form.

COCORITE SAVANNAS OF THE NORTHERN PLAIN

In certain parts of the northern plain occur grasslands characterized by the presence of the cocorite palm, *Maximiliana elegans* Karst., and known to have succeeded forest within the last half-century due to repeated fires set by the shifting cultivator and cane farmer. These grasslands lie on the western part of the northern plain where the rainfall is relatively low so that the vegetation often dries up enough to burn easily in the dry season. They are in the same district as the Piarco group of savannas and occupy similar alluvial terraces, being similarly rather flat

and illdrained and having similar impeded soils. The former forest was of the same Carapa-Eschweilera type as surrounded the Piarco and other savannas, conditions on the sites of these cocorite grasslands being in fact substantially equal to those of such surrounding forests. The soil drainage is bad, but just not too bad to support forest.

The dominant grass is always *Imperata brasiliensis* Trin., associated with *Arundinella confinis* Hitchc. & Chase, *Paspalum pilosum* Roth., and sundry *Andropogon* spp.—*A. bicornis* L., *A. selloanus* (Hack.) Hack., and *A. leucostachyus* HBK. *Heliconia psittacorum* L., is generally very abundant. Woody growth consists typically of an occasional fire-blackened Maximiliana palm (Fig. 10) and scattered bushes or little trees (most of which have sprouted from an old root stock since the last fire) of *Coccoloba latifolia* Lam., *Cordia cylindrostachya* (R. & P.) R. & S., *Tabebuia serratifolia* (Vahl) Nichols., *Terminalia amazonia* (J. F. Gmel.) Exell., *Protium insigne* Engl., *Vismia* spp., and Melastomaceae. The flora is quite different from that of the savannas previously described.

FIG. 10. Fire grassland of Imperata on the northern plain of Trinidad with Maximiliana palms as relics of the original forest.

THE VENEZUELAN LLANOS

THE MESA OF GUANIPA

During the two days February 10th-11th, 1945, the writer travelled by road from Ciudad Bolívar on the Orinoco River to Caracas, a distance of 480 mi. The most part of this journey is across the great llanos, plains sloping down to the Orinoco in the south and formed of Plio-Pleistocene alluvial deposits. From Soledad on the north bank of the Orinoco opposite Ciudad Bolívar, through El Tigre and almost to Pariaguan (about 90 mi.) the road traverses various so-called "mesas," the Mesa de Guanipa and others, which are savanna country *par excellence*. From Pariaguan to El Sombrero in the foothills of the northern Cordillera (250 mi.) the road crosses the *alto llano*, a transitional zone between flat savanna country to the south and more dissected, geologically older, bush-covered country to the north. The mesas traversed lower down are so-called because they are slightly elevated sections of the plains, in the form of huge terraces, which are not subject to inundation in the rainy season. The mesas are bordered by small scarp faces fronting towards rivers and are dissected by occasional trough-shaped valleys.

The road out of Soledad runs north-eastward in a straight line for mile upon mile across broad, even, very gently inclined expanses with scarcely a sign of a ravine or river bed breaking the sweeping monotony of the landscape (Fig. 11). The whole area is covered with bunch-grass savanna dotted with occasional trees of *Curatella americana* L., *Bowdichia virgilioides* HBK., *Byrsonima crassifolia* HBK., and *Roupala complicata* HBK. Such tree-dotted savanna is commonly known in Venezuela as *chaparral* from the most abundant tree, *chaparro* (*Curatella*, a name transferred from the European Cork Oak, *Quercus suber*). Chapparal both in Spain and North America has a meaning quite different from this in Venezuela. Trees are about 30 yards apart on the average and reach a much greater size than on the Trinidad savannas, up to 20 ft. high and often with a definite trunk 1 ft. in diameter. They retain, however, their gnarled habit and have rounded crowns.

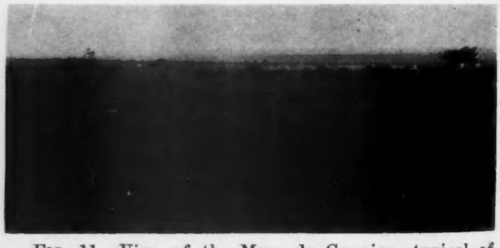

FIG. 11. View of the Mesa de Guanipa, typical of vast areas of the Orinoco *llanos*. Trees are Curatella and Byrsonima.

This region has recently been studied botanically in some detail by Pittier (1942) who listed 44 species of grasses out of 109 species of plants comprising the savanna association.

Five of the 44 grass species attain sufficient abundance in certain parts to be called dominants. *Leptocoryphium lanatum* is dominant on low ground where the soil is not sandy: it is relatively rarely en-

countered. *Trachypogon vestitus* and *Axonopus chrysodactylus* occupy depressions where sand has collected and is deepest. *Trachypogon montufari* and *T. plumosus* are found on the sloping ground with a clay or gravel topsoil. These are the dominants of the ordinary plateau surface of the Mesa. A change occurs on river flats bordering the rivers and streams which have cut trench-like valleys into the Mesa. Here Trachypogon and Axonopus disappear and give way to *Mesosetum chaseae,* 5 species of Paspalum and *Sporobolus indicus.* The bunch-grass character of the savanna is less plainly marked and the grasses are finer and more delicate.

Cyperaceae are well represented. *Dichromena ciliata* is ubiquitous and here and there one finds a peculiar little plant, *Oncostylis* (*Bulbostylis*) *paradoxa,* which has a little woody aerial rhizome sheathed with old leaf bases. Termite mounds like those of the Trinidad savannas are seen with a like frequency.

The savanna soil is a loose, yellow sand usually about a foot deep, overlying a hard and compact red clay. The surface is never "hogwallowed." Stones are are rarely seen and when they occur they are of ironstone. Here and there occasional low knolls disturb the plain and these are seen to be capped with a layer of coarse ironstone gravel up to a foot or more in thickness lying upon the red clay. These knolls are virtually treeless and their herbaceous vegetation is markedly scanty. After passing through El Tigre the road crosses country which grows progressively flatter and more open, the savanna trees becoming smaller and extremely scattered, and opening up wide views of the country. Whole stretches are absolutely bare of trees. There is the same sandy topsoil, the same occasional knolls capped with ironstone gravel or massive ferruginous conglomerate. No termite mounds were seen here.

The rainfall of the Mesa de Guanipa, as given by Pittier (1942), for the 9 years 1933-41 varied from 26.3 to 64.7 in. per annum. Average figures for the period showed an annual precipitation of 43.8 in. distributed in a wet and a dry season of which the former lasted 5 months (June-October) with 5 to 7 in. per month and the latter 7 months with under 4 in., 3 months receiving ½ in. or less. The actual figures are:

Jan.	Feb.	Mar.	Apr.	May	June	July
26	5	13	14	93	167	173
1.0	.2	.5	.6	3.6	6.7	6.9

Aug.	Sept.	Oct.	Nov.	Dec.	Total
194	152	123	92	43	1095 mm
7.7	6.0	4.9	3.6	1.7	43.8 in.

There appears to be no reason why this should not be considered a forest climate which, given favorable soil conditions, would support a deciduous seasonal forest such as is actually found a little further to the northward. Pittier did not put forward any theory to account for the presence of grassland on the Mesa, though he evidently discounted recent origin due to fire stating "these savannas have never been covered with forests" (p. 14). It would appear from general inference that he attributed the lack of tree vegetation to the infertility of the soil.

MORICHALES AND GALLERY FORESTS

The rivers which meander across the llanos in trough valleys between the mesas are bordered by *morichales,* that is, by groves of Mauritia palms. Pittier (1942) described the typical *morichal* as follows (translation):

"These ravines are marked at least by dense thickets from which arise slender *moriches,* at first more or less isolated, but which soon form on both banks of the stream a continuous belt of variable width, broken by open swamps in which grow thickly the erect stems of *Montrichardia arborescens.* The number of species which grow within the *morichales* of the Mesa of Guanipa appears very limited for the crowded palm trees form a closed canopy which hinders the passage of light. . . ."

Pittier noted only 9 plant species in the *morichal* of which three were palms (Mauritia, Euterpe, Bactris). Associated with the *morichal* proper he noted areas of herbaceous swamp dominated by grass and sedge, and along certain streams *dry morichales* which appear to be transitional between pure *morichal* and woodland. All this vegetation is clearly swamp, associated with a perennially high watertable. It duplicates exactly certain swamp vegetation in the Blanquizales Lagoon in Trinidad (Beard 1946).

Gallery forests are very little seen in the Venezuelan llanos. One commonly imagines strips of tall, evergreen forest bordering the rivers when thinking of savanna country but in this region *morichales* for the most part replace them.

THE UPPER LLANO

Shortly before reaching Pariaguan the road descends from the Mesa of Guanipa across the head of the Rio Pao—bordered by a *morichal*—and enters a tall, dense chaparral. The Curatella and other trees are up to 30 ft. in height, though retaining their curious gnarled form, and grow thickly so as almost to touch one another. Occasional Acrocomia palms join the assemblage and the grass ground cover is somewhat reduced. This community is strongly suggestive in appearance of examples the writer has seen of the African *miombo* (Isoberlinia-Brachystegia woodland). Beyond Pariaguan the country is much more undulating than on the Mesa and as the brokenness increases the high chaparral merges into a true deciduous seasonal forest which was leafless at the season of the writer's visit. This is normal, dissected, forest country and the soil appeared as a red-weathering clay at the surface. Some

distance further on the country flattens out again and the forest is joined by numbers of a small palmetto (*Copernicia tectorum*) which eventually comes to form on level stretches a palm savanna, grassland scattered with these palmettoes instead of with Curatella and its associates. This palmaceous vegetation should not be confused with the *morichal*. Mauritia grows to be a tall, slender palm in dense stands along river banks. Copernicia is a short fuzzy palmetto and occurs irregularly scattered singly and in pairs across savanna country, given certain soil conditions (Fig. 12).

FIG. 12. Palm savanna with *Copernicia tectorum* on flats of the upper *llanos*. Ground burnt clean in the foreground.

Copernicia is seldom absent from the landscape all the rest of the way across the *alto llano* to El Sombrero. The country is variable, now flat, now undulating and in sympathy the vegetation varies constantly between deciduous forest, thorn bush, chaparral and palm savanna. The sand-capped soils of the Mesa are no longer seen and the red-weathering clay shows everywhere at the surface though many of the hill crests tend to be capped still with ironstone gravel. Where this gravel capping is thick, the chaparral is seen. Otherwise the hilly and sloping land is covered by forest or by thorn bush which represents forest degraded by man's interference. The palm savanna comes in on swampy levels with the deciduous forest appearing again as a narrow gallery forest along streams. At the time of the writer's visit the clay soil of the palm savannas was dry, hard and cracked but had the appearance of being waterlogged in the rainy season. The surface is slightly hogwallowed.

MYERS' JOURNEY TO SAN FERNANDO

In his journey to San Fernando de Apure in 1930-31 Myers (1933) observed the same succession of types. He travelled by road from Caracas via San Juan de los Morros, Ortiz, El Sombrero and Calabozo and thus passed through the whole transition from the mountains to the lowest river flood plains.

"South of San Juan de los Morros," wrote Myers, "one passes through large continuous areas of a low, open type of forest. Some of this is definite thorn forest, with *Acacia macracantha* H.B., dominant, but the larger area, consisting of taller, now largely leafless trees, approaches more to a monsoon type. The rainfall, of which there are unfortunately no records, can only be about 40 in., thus falling much below that required for monsoon forest in Schimper's definition (70 in.). It agrees better with his savanna-forest, to which he actually refers it (1903, p. 352), but I consider the term very misleading, since none of the typical savannah trees or shrubs, such as *Curatella*, *Bowdichia* and *Byrsonima* are present. It is probably best to follow Troup (in Tansley and Chipp 1926 p. 292) and call this merely "deciduous forest" until a better classification can be drawn up."

The present writer has described this type of forest as "deciduous seasonal forest" and regards the thorn bush as a secondary stage due to the shifting cultivator. The term "savannah-forest" would certainly be very misleading, though it could perhaps be applied to the transitional bush between forest and savanna which the writer saw near Pariaguan, where the savanna trees closed up almost to form a forest. Any such broad intermediate stage is, actually, very rare in the northern tropics and the writer has never seen another example. It seems to be more common in Brazil, passing by the names Catanduva in Warming (1892) and Cerradão in Waibel (1948).

The higher llanos from El Sombrero to Calabozo, as reported by Myers, agree with those seen by the writer from Pariaguan to El Sombrero. Deciduous seasonal forest alternates with orchard savanna bearing *Curatella americana* and *Bowdichia virgilioides* or Copernicia palms, with *Cymbopogon rufus* as the dominant grass.

After leaving Calabozo, Myers crossed the true lower llanos which the writer missed in journeying up from Ciudad Bolívar since at the start on the Orinoco the road was already on one of the Mesas. "This plain," he wrote, "opens out still more and we see for the first time a view such as inspired Humboldt's classical description of the llanos—an apparently limitless expanse of grass as flat as the sea, with the hazy presence of a few scattered trees on one horizon only, barely discernible. This is evidently typical low bunch-grass savannah."

Cymbopogon rufus was still the dominant grass, giving way in places to *Andropogon condensatus*. A herb, a blue-flowered Labiate, *Hyptis suaveolens* was always conspicuous and in places assumed complete dominance for miles. This appeared to be due to the effect of heavy grazing. In places the savanna was absolutely treeless, in places with Copernicia palms and in places with Curatella and Bowdichia shrubs. Occasional belts of "low, open deciduous forest, with a most unusual abundance of strangling figs (*Ficus* sp.)" were crossed. As the road approached nearer to the Apure and Portuguesa rivers the plains showed signs of inundation in the rainy season. These flats were treeless save for a bush, *Ipomoea crassicaulis*, and the grasses were short and differed from those of the Cymbopogon savanna. *Sporobolus indicus* and *Steirachne diandra* were noted. Lower still in the llanos the route crossed the zone of the *esteros*, wide shallow depressions covered

with standing water in the rainy season and still moist enough throughout the dry season to enable growth of the grasses. The grass cover of these *esteros* is markedly distinctive, "a pure knee high stand of a much stouter grass with long trailing stems rooting at the nodes, and close, leafy, sterile culms, erect and somewhat hirsute. Although no flowers were to be found, this grass is undoubtedly *Paspalum fasciculatum* Willd."

"Apart from the fringing forest along this river (the Portuguesa) and one palmetum (*Copernicia*) near San Fernando de Apure, the route from Camaguan to the latter town, on the banks of the Apure passes through practically nothing but vast plains of *Paspalum fasciculatum*, up to waist and even breast-high. Occasional damper areas and lagoons support stands of *Ipomoea crassicaulis*. On dryish areas there are stretches of *Malachra alceifolia* Jacq. The *Paspalum* covers dried, cracking mud. Rarely, among its close-growing sterile culms, appears a flowering stem of another, more slender grass, *Eriochloa punctata* (L.) Desv. Hamilt."

Here for the first time Myers mentions the nature of the soil, "dried, cracking mud." This is evidently quite different from the sand-over-clay soil of the higher llanos and presumably consists of recent alluvium of which a fresh film is deposited every year.

Myers considered this Paspalum grassland as "true high-grass tropical savannah" according to Bews' classification (1929).

THE LLANOS IN COLOMBIA

The great savanna-covered plains of the left bank of the Orinoco extend far to the south-west into Colombia. According to Dugand (1945) and Bates (1948) the ultimate boundary is the Guaviare River, one of the tributaries of the Orinoco, beyond which the Amazonian rain forest is entered. Dugand described the predominating vegetation as "immense grassy savannas, dotted with palms and scattered shrubs." Patches of forest and groves of Mauritia palms occur in "humid bottom-lands" and there are extensive gallery forests along the rivers. Photographs by Bates demonstrate the association of these savannas with quarternary terraces.

THE NORTHERN CORDILLERA OF VENEZUELA

The highway from Ciudad Bolívar to Caracas, after crossing 600 kms. of plains country, reaches at Ortiz the foothills of the northern cordillera, a great series of mountain ranges which rises east of Barquisimeto and runs eastward bordering the Caribbean Sea for several hundred miles. This is not properly a section of the Andes, being detached therefrom and taking a totally different direction. The highest peaks exceed 9,000 ft. and in the centre the ranges include a basin of interior drainage containing the Lake of Valencia lying some 1500 ft. above sea level. This region is the most densely populated in Venezuela and has been the longest settled. Accordingly, since Venezuelans are particularly careless in their treatment of natural resources, there are abundant signs of devastation by humans. The region has a low rainfall since the coastal ridge is the highest and catches the rain from the prevailing north-east winds, setting up a rain shadow in its lee. This leads annually to a vast outbreak of fires in the dry season and the mountain slopes which are known from early accounts to have been formerly covered with forest are now largely covered with grass.

The town of San Juan de los Morros is set in the midst of mountains rising 3-4,000 ft. above it. The "Morros" from which the town is named are limestone pinnacles which have stood out in the form of "haystack hills" or "mogotes" as they are called in Cuba, after erosion has removed the surrounding schistose rocks. They are spectacular and are not the only examples in this district, which might be termed the Venezuelan Dolomites. The limestone is covered with a thin woody scrub but the neighboring schist mountains have been almost entirely denuded right to their summits and are covered with grass, with occasional shrubs. At the time of the writer's visit in February slopes were extensively fire-blackened. Around the Lake of Valencia the mountains are similarly grass-covered up to a height of 5-6,000 ft. on the northern or seaward range. Above this height a belt of cloud is usually present and with it there is an abrupt transition to evergreen forest. Since their denudation the mountains have evidently been severely eroded. Between Caracas and Los Teques the mountains are covered with poor xerophytic scrub full of cactus and agave rather than with grass, but immediately to the north of Caracas itself the steep lofty Avila range is grassed up to the cloud belt at 5,000 ft. above sea level.

The vegetation of the Caracas valley was described by Tamayo in 1943. The average annual rainfall he gives as 824 mm (34.3 in.) but precipitation is very erratic, and has varied between 459 mm (18.7 in.) and 1244 mm (51.8 in.) per annum. Soils are developed either over schist or over limestone, with grassy vegetation predominant on the former and a scrub of cacti, agaves and leguminous bushes on the latter. From all accounts and inferences the entire region was formerly covered with forest which has gradually disappeared due to cutting, fire and grazing. Various stages of degradation can still be seen: deciduous forest, thorn bush, *"crassuletum"* of *Cordia curassavica* and finally savanna or cactus scrub. Tamayo gives a long list of constituent species for two types of savanna, but it is not clear which are the dominants or the most abundant unless these should be the species appearing first on the list. On the tops of the ridges *Aristida adscencionis, Eragrostis trichocolea, Paspalum notatum, Sporobolus indicus* and *Cipella linearis* achieve first mention. Shrubby constituents include four melastomes, *Clidemia ciliata, Miconia albicans, M. rubiginosa* and *M. rufescens.* Savanna of slopes and lower parts of hills is evidently richer and features three species of *Andropogon,* five of *Aristida,* three of *Paspalum* and *Trachypogon plumosus.* Tamayo mentions elsewhere that "chaparro" is present in the savannas but his list

does not include *Curatella americana*. Pittier (1939), however, mentions this species which is certainly present, as the writer has seen for himself, together with a Roupala and *Oyedaea verbesinoides*. During the degradation process the hills, which are very steep, appear to have become severely eroded and for the most part there is now very little soil, the vegetation having little between it and the bedrock. This erosive process continues since the grasses are nearly all of the bunch-grass type and do not form a continuous turf.

These grasslands are clearly of recent origin due to human influence and seem closely comparable to the St. Joseph savanna of Trinidad.

In the Andes proper substantial areas of mountain slopes formerly covered with forest, at all elevations from the foothills up to the *páramos* at 10,000 ft., have been converted into grassland by fire and grazing since the arrival of Europeans. Such areas may be excluded from this study of natural grasslands of the lowland tropics.

The West Indies

THE LESSER ANTILLES

The Lesser Antilles are a festoon of small oceanic islands disposed between Trinidad and Puerto Rico at the eastern end of the Caribbean Sea. For the most part they are high, volcanic and mountainous, though some of the offlying islands are low and formed of limestones. The vegetation throughout is typically forest of one type or another, developed under rainfalls varying from 40 to 400 in. per annum and on a variety of soils and sites. Grasslands other than strictly artificial pastures occur only on three islands, Dominica, Antigua and Barbuda. On the last named only is there any indication of natural savanna. Fuller details of the vegetation of these islands are available (Beard 1947).

DOMINICA

Dominica is an exceedingly mountainous volcanic island with an area of 304 sq. mi. within which there are five peaks over 4,000 ft. high and a great number number exceeding 3,000 ft. The rainfall in the interior is very high, over 300 in. a year having been recorded in gauges, and the greater part of the island is or was originally covered in high, dense rain forest. Only on a narrow strip down the west or leeward coast does the rainfall become too low to support rain forest, decreasing to some 60 in. annually. All the original forests in this part have been destroyed, but the widespread areas of secondary bush indicate by their composition that some kind of sclerophyll or "dry evergreen" forest was formerly present. In the centre of this coast there is a district called the Grand Savanna where a good deal of grassland is mixed with the bush in large patches.

The principal savanna area is on a promontory sloping gently up from sea level to a height of several hundred feet but the grasslands also ascend the mountain slopes and cover certain upland plateaus overlooking the coast at a height of about 600 ft. The soil throughout is of the type known as shoal (Hardy 1941). The area is burnt annually.

The dominant grass throughout appears to be *Sporobolus indicus*, associated with an Andropogon and a sedge. Some woody growth is always present in the savannas and is very variable. One phase comprises low shrubs of *Byrsonima lucida* up to 5 ft. high and *Stigmaphyllon cordifolium* up to 2½ ft., the latter normally a vine but here assuming a shrubby habit. A species of *Heliotropium* associates freely with the grass here. Elsewhere, isolated trees of the introduced logwood (*Haematoxylon campechianum*) or of *Tabebuia pallida* are seen, or the savanna is plentifully dotted with *Guettarda scabra*, a forest tree here assuming a suffrutescent habit. This last is most characteristic of the upland plateaus. The savannas are mixed with patches of degraded bush containing mostly Haematoxylon and species of *Croton*.

The soil here exhibits impeded drainage and the natural conditions are in many ways not unlike those typical of savanna lands. With the exception of the *Byrsonima lucida* phase, however, we are obviously dealing with fire-degraded woodland and this is probably true for the entire area. None of the typical elements of American savannas except *Sporobolis indicus* are present here and in the writer's opinion the area was formerly all forested.

ANTIGUA

Antigua is a more or less lowlying island in the Leeward group, of some 108 sq. mi. It includes a range of old volcanic hills up to 1,200 ft. high but the greater part is formed of sedimentary lowlands less than 300 ft. in elevation. All the island was formerly cultivated in sugar but certain areas of the less tractable soils have been abandoned and are mostly now used for grazing cattle. The general appearance of these areas, according to Charter (1937) is "course grassland scattered over with small patches of scrub. The dominant grasses on these areas are species of *Paspalum* and *Andropogon* and include *P. plicatulum*, Michx., *P. secans* Hitchc. & Chase, *P. notatum* Flügge, *A. glomeratus* (Walt.) BSP. and *A. saccharoides* Sw." Unless such pastures are given frequent attention they rapidly become covered with a dense growth of thorn trees, principally *Prosopis chilensis*, *Acacia nilotica* and several other Acacia species. The cattle themselves spread the thorn bush by browsing the seed pods and so distributing the seeds in their dung. All stages in the growth of thorn bush can be seen, from the still grazed pasture with small thorn shrubs to the dense and impenetrable thicket and finally, after the axe has been at work, to the "thorn savanna"—a fresh pasture with scattered Prosopis and Acacia as shade trees (Fig. 13). This forms a landscape strongly reminiscent of African "thorn veld," but is entirely artificial and owes its existence to man and cattle. There is no doubt that all Antigua soils were formerly forested, and when abandoned to bush directly from cultivation they come up in secondary woodland without

FIG. 13. Thorn bush in Antigua with *Prosopis chilensis* and *Acacia* spp., grazed pasture beneath.

FIG. 14. Barbuda: mixture of grassy glades and patches of bushland. Right to left: open patch which is a rain puddle in wet weather, grass, bushes of Eugenia, Comocladia, etc., spiky Plumeria tree and Bucida behind.

Acacias. These latter are a feature of grazed land only and all of the species concerned are introductions from outside.

BARBUDA

Barbuda is a small island with an area of only about 35 sq. mi., scantily populated and composed of a series of flat limestone terraces rising in the centre to a height of about 100 ft. Two thirds of the island consists of a flat plain less than 10 ft. above sea level. Rainfall is low and erratic, having varied (since 1920) between 26 and 61 in. per annum, with an average of 36 in. Long droughts occur and the island is severely windswept. The underlying coral limestone carries very little depth of soil. Frequently it is exposed and forms a bare pavement, with soil only in the pockets, potholes and crevices between the slabs. The soil, such as it is, is a stiff clay varying in color from black on the lowest lands to red on the highest. There are no rivers or ravines and the soils on the lower sites are waterlogged after rain.

In view of these adverse conditions it is natural to find that the most widespread type of vegetation on Barbuda is Warming's "Evergreen Bushland" (1909)—"a grey, desolate, useless and scorching bushland, between whose thorny shrubs and small trees one cannot penetrate without the aid of an axe." The bushland is from 10 to 30 ft. high, composed of gnarled little trees and bushes with small, hard, evergreen leaves. It does not seem to have been much disturbed by man except near the village.

On the marginal plain the dominant tree in the bushland is *Bucida buceras*, associated with *Tabebuia pallida, Coccoloba diversifolia, Byrsonima lucida, Guettarda scabra, Pisonia fragrans* and many others, including a Coccothrinax palm. On the southeastern part of the plain drainage seems to be at its worst, leading to the appearance of extensive pockets of savanna. Changes in site drainage, apparently quite slight, lead to abrupt alternations of bushland and grassland. The savannas are quite treeless and composed of *Paspalum bakeri*, a bunch-grass with coarse, cutting leaves growing in well developed tussocks. The savannas occur as glades varying in extent from several acres down to a few square yards. The larger ones are bordered always by Bucida trees assuming a domed form with long branches given off from the base, loaded with bromeliads (*Tillandsia utriculata*). Smaller glades pass directly into bushland (Fig. 14). The whole area is an irregular mosaic of glades of savanna, scattered, domed Bucida trees, patches of saplings (mainly Myrtaceae) and clumps of trees with cacti and palmettoes. These alternations seem to be dictated solely by very slight changes in relief and soil depth. The savannas occupy slight depressions where water collects in wet weather and the woodlands cover the slight rises. The savannas are alternately waterlogged and dried out, while the woodland sites are less prone to waterlogging, better aerated and with effectively more root room. Deeper depressions in the plain which are more or less constantly under water are filled with sedge (*Fimbristylis ferruginea*) and bushes of *Annona glabra*.

There can be no doubt that these savannas are of natural origin and their association with soil drainage conditions is clear. Fire seems to be unknown.

THE GREATER ANTILLES

The Greater Antilles comprise essentially the four major West Indian islands of Puerto Rico, Hispaniola (including Haiti and the Dominican Republic), Jamaica and Cuba. Where there are mountain ranges or other broken country on these islands, the vegetation is or was typically forest. Where there are plains of large extent with mature soils, the vegetation is typically savanna.

No natural savannas are known from Puerto Rico or Jamaica, being relatively small mountainous islands, though in the latter there are in many of the drier parts grazing areas with thorn bush similar to those of Antigua. These are similarly artificial and represent a degradation of deciduous forest. There are certain savanna areas in Hispaniola and wide extents of savanna in Cuba, situated on plains in those islands.

HISPANIOLA

This large island is divided politically by a north-

south boundary between Haiti and the Dominican Republic, but the natural features run the other way in the long axis of the island and cross the political frontier.

The island is traversed by a number of mountain chains running more or less in an east-west direction and containing the highest peaks in the Antilles with a maximum elevation of 10,000 ft. Between the ranges there are flatter lands at various elevations, comprising one rather extensive central plateau and several smaller plateaus or plains. The bulk of the island is, or was, forested, most of the forest being of a xerophytic nature due to inadequate rainfall (20 to 50 in. annually). In the mountains there are moist evergreen forests, and also pine forests whose ecology presents interesting problems. There are savannas on the plains and plateaus.

The writer has unfortunately been unable to consult the solitary modern ecological work on the vegetation of the island, Ciferri's "Studio geobotanico dell' Isola Hispaniola" (1936). Dr. J. T. Curtis, of the University of Wisconsin, has, however, been kind enough to supply information on the savannas of Haiti from his own observations, in considerable detail, and the data which follow are taken from his letters. Dr. Curtis distinguishes three types of savanna, "open," "orchard" and "dry."

Open Savanna covers an area of 80,000-100,000 acres on the Central Plain at an elevation of some 1,700 ft. above sea level. The region is unpopulated, primarily because of the severe annual fires and also because of the scarcity of water in the dry season. The rainfall varies from an average minimum of only ¼ in. in February to 8¼ in. in June, with an annual total of 48½ in. (1167 mm.). The dry season lasts from November to April, during which less than 4 in. of rain a month fall. No records of temperature are available, but there is certainly no frost at any time. Dr. Curtis estimates the extreme minimum temperature at 45°-50° F. Streams are infrequent and deeply entrenched, the surface of the plateau level to gently undulating.

The soil profile was studied in connection with attempts to grow Cryptostegia and revealed a uniform black surface horizon 28 to 36 in. deep, grading into a grey or almost white impervious hardpan layer of 6 to 10 in. thickness. This was underlain by weathered rock material. The hardpan was hard only in the dry season. In the rainy season, the overlying black layer was very wet, almost boggy, and the white layer was soft but still apparently impervious. The latter was of a gley-like appearance, in places having reduced iron spots or mottles. Test plots of Cryptostegia died out completely in the dry season, and Dr. Curtis is of the opinion that woody plants in general would have difficulty in penetrating the hardpan layer.

There is a spring-like resurgence of growth when the rainy season commences. It is marked by the appearance of many showy flowers, most coming from bulbs or fleshy roots and rootstocks. Among the forbs noted were *Zephyranthes eggersiana, Stenorrhynchus orchioides, Lobelia domingensis* (?), *Polygala* sp., *Stigmatophyllum* sp., *Euphorbia prostrata* (?), and *Crotalaria* sp. There are no trees. The dominant grass over large areas, in which it grows in a nearly pure stand, is *Themeda quadrivalvis.* Other grasses and grass-like plants collected on the savanna by Dr. Curtis and identified by Mrs. Agnes Chase were *Andropogon bicornis, Andropogon tener, Aristida refracta, Paspalum milligrana, Paspalum plicatulum, Paspalum densum, Sorghastrum parviflorum, Fimbristylis diphylla, Fimbristylis monostachya, Scleria hirtella* and *Scleria pterota.*

Orchard Savanna includes savanna with pine (*Pinus occidentalis*) as well as with the typical orchard trees (Curatella, Byrsonima, Anacardium) since Dr. Curtis says that here at any rate they mingle and cannot be separated. The orchard savanna is also seen on the central plain, on its eastern and south-eastern part where the ground is more broken. The north-western portion is open grassland on a gently rounding, undissected plateau, as described above. The only trees are along the few ravines or draws present and hence there are great areas with no trees whatsoever. The country where the orchard savanna appears is deeply dissected, the ravine bottoms are wooded and the intervening country is under savanna with scattered trees, the open grassland still being seen on hilltops which represent relics of the dissected plateau surface. The orchard type appears to be associated with topography in process of rejuvenation, where drainage conditions have improved slightly from the flat country of the open grassland. Fully mature topography, which Dr. Curtis calls "Knob-hill country" is covered with xerophilous bush containing pines and small hard-leaved evergreen trees, with Themeda grassland or patches of shrubs (Pictetia, Brya) in the valleys between the "Knobs." The position is now reversed, with grass and not trees along the bottomlands. The bush clustered on the tops and sides of the "Knobs" is apparently somewhat open and, except for the pines, of low stature. *Pinus occidentalis* is typical, with *Coccoloba rotundifolia, Acacia scleroxyla, Pisonia domingensis, Comocladia* sp. and *Coccothrinax argentea.* Dr. Curtis states that grass is ecologically dominant. The soil is a heavy yellow clay from limestone bedrock. No details are available on the soils of the orchard savanna, other than that they do not show the surface black horizon. Dr. Curtis is of the opinion that this type is the result of fire rather than of climatic and soil conditions.

Dry Savanna is found on Miocene limestone on the low foothills near the ocean in regions of 20 to 30 in. annual rainfall with a severe dry season. Almost no soil is present, the substratum consisting of rock detritus. This is due in part to the considerable surface drainage so that at no time, even in the rainy season, is the ground wet for more than a few hours. The typical grass is *Uniola virgata,* in many places the only grass. Another grass on the more level areas is *Bouteloua heterostega. Agave antillana* is well distributed. The shrubs are *Plumeria alba,*

Maytenus buxifolia, Schaefferia ephedroides and *Jacquinia berteroi.* An unimportant but characteristic and widespread plant is the orchid *Tetramicra ekmani,* epiphytic on the Uniola clumps. Judging by old French records, says Dr. Curtis, this savanna was present in 1750; even so, it may originally have been of fire origin. In any case, it is now stable, and has little prospect of successional change, regardless of fire.

The presence of pine savanna in Hispaniola brings forward interesting ecological problems in connection with the distribution of the pine in question, *Pinus occidentalis,* in the island. This pine is found on a great variety of soils and geological formations, on a diversity of landscape and at altitudes ranging from 500 to 10,000 ft. above sea level. It tends to occur in more or less pure stands with a grassy ground cover beneath, but in by no means the majority of cases could the vegetation be termed pine savanna. As Chardón (1941) has pointed out, the real domain of the pine lies above the contour of 2,000 m. where it covers wide areas in the central cordillera and more southerly ranges, forming absolutely pure stands above a carpet of the grass *Danthonia domingensis.* This behavior is limited to mountains where the climate is seasonally dry enough to encourage forest fires, and according to Holdridge (1945) there is reason to believe that the pine has succeeded various types of mixed montane forest as a result of burning. Where fires are prevented for several years, he states, hardwood seedlings start coming up in the understory. Such pine forests, though grass carpeted, are not pine savanna, since the grass is not ecologically dominant. True pine savannas are found only in the lowlands and foothills where the pine is much less widespread and occurs in limited areas forming much more open stands. The lowland vegetation, it seems, has more resistance to fire and to the invasion of the pine which is only able to penetrate depauperate communities such as orchard savanna and dry evergreen scrub. We may regard the pine as a fairly recent colonist from North America which has sought to establish itself wherever it could find favorable conditions. Fires set in the high mountains by the aboriginal Arawaks or by lightning led to its wide extension there, and in the lowlands it became a component of preexisting orchard savannas and scrubby communities. The species is evidently extremely tolerant and also fire resistant and these two qualities enabled it to add itself to the aborescent members of the savanna community. Pine savanna should probably be regarded as only a variant of the orchard type.

In the Dominican Republic, according to Chardón, the pines where they occur at low elevations, often are mixed with considerable groups of *Byrsonima crassifolia, Chrysophyllum olivaeforme* and *Eugenia* sp. and the grass cover is provided by Andropogon. Such areas are probably closely similar to the Nipe plateau of Cuba of which we have a detailed description (Carabia 1945), reviewed in the following section.

CUBA

Cuba is the largest of the Greater Antilles, an island 720 mi. in length, and is replete with savanna lands. No satisfactory detailed ecological study of the vegetation exists but the writer has drawn upon Seifriz's (1944) "Plant Life of Cuba" (a useful work though somewhat generalized, and botanical rather than ecological) as well as on the travels of Brothers Marie-Victorin and León (1942, 1944), which yield many interesting botanical details. Carabia's "Vegetation of the Nipe Plateau" (1945) is a useful local study of a complex area. For study of savannas, the most fruitful work of all is Bennett & Allison's "Soils of Cuba" (1928) which gives very thorough data on savanna and forest soils as well as notes on the vegetation types. Thanks to this, in conjunction with Charter's soil work in British Honduras, to be discussed in the next section, we understand these savannas more thoroughly than any others in tropical America.

Cuba lies just within the tropics, between 20° and 23° north latitude. The climate is a typical moist tropical one, with the average temperatures for all months of the year lying between 70° and 80° F. Frost has never been reliably recorded. The greater part of the island receives an annual rainfall of between 40 and 60 in., a few very limited areas receiving less, and the mountain chains locally attracting more. Distribution is fairly consistent throughout the island, entailing a dry season from November to April, during which which generally from 1 to 4 in. of rain a month are received, and a wet season from May to October, with from 4 to 10 in. of rain a month. The rainy season has two maxima but the drop in between is insufficient to constitute a second dry season. The dry season is a severe one and consequently the vegetation, except in the mountains, is mainly xerophytic.

Geophysically, Cuba consists of a low, continuous plain rarely raised 200 ft. above sea level and floored with Tertiary deposits, through which rise here and there isolated hill and mountain masses of older Tertiary and Cretaceous sediments and igneous intrusions, rising to a maximum elevation of some 7,000 ft. The hills and mountains fall roughly into five groups. At the western end are the Organ Mountains, formed of cavernous limestones which stand out typically as "haystack hills" or "mogotes." Three groups of hills and low mountains, mainly igneous, occur in the centre, in Santa Clara Province, and another range of low hills in Camagüey. Finally at the eastern end of the island is the great Sierra Maestra of lofty peaks with associated ranges such as the Sierra de Nipe.

The mountains of the island, with the exception of the Sierra de Nipe, are or were covered with forest, the soil-less limestones of the Organ Mountains with a low, highly xeromorphic growth, the low mountains of the centre and the foothills of the eastern mountains with seasonal forests and the higher elevations of the eastern group with montane forests —rain forest and elfin woodland. The Sierra de

Nipe features certain pine savannas and will be discussed further.

The plains fell originally into three categories, swamps, savannas and well-drained forests. In this island, savanna is typically the vegetation of plains, though not of all plains. Bennett & Allison wrote: "Predominantly, savannas are somewhat to very flat: there are also undulating areas but very rarely is relief stronger than this." Much of the swamp and savanna land remains in its original condition, but the bulk of the forest land has been cleared for agriculture. Relics indicate for the most part the former occurrence of deciduous seasonal forest. From the earliest times in Cuba it was appreciated that there are essential differences between forest and savanna soils, the savannas being infertile and seldom lending themselves to the production of crops.

So well recognized is this fact that Bennett & Allison could write that "in Cuba the term savanna, as applied to land, carries both a vegetative and a soil meaning. . . . As a rule the savanna lands have at relatively shallow depths subsoils composed of material which affects the soil moisture conditions unfavorably." Marie-Victorin & León expressed it: "One calls savanna, in this country, a stretch of non-mountainous terrain, with poor soil, with herbaceous or shrubby vegetation in a natural state." It is not even suggested that the savannas have a climatic relationship. Scattered as they are throughout the island mixed with forest (or potential forest) country and receiving a rainfall which though sometimes meagre is nearly everywhere adequate to support forest of some kind, the climatic explanation does not suggest itself. On the other hand the intricate relation between the savannas and special conditions of soil and landform is arrestingly obvious. Generally, the soils feature a permeable horizon overlying an impermeable subsoil. Sometimes this effect is due to the presence of rock which has not decayed deeply, sometimes to the superposition of a sand upon a clay horizon, sometimes to the occurrence of layers of pebbly ironstone concretions (perdigón) or massive ironstone sheeting (mocarrero). Drainage impedance is accentuated by the low relief. Savannas, therefore, occupy portions of the plains where these special soil conditions have developed. Bennett & Allison's soil map indicates that more than one third of the Cuban plains is savanna country. The soil pattern is repeated over and over again. The Santo Domingo savanna is on sand (with or without ironstone) over clay over chalk. The coastal savannas of the Trinidad plains show a sandy loam over mottled clay containing quartz gravel. On the Camaguey plain there is the Oriente clay, a forest soil (black clay over whitish clay over chalk) and also the Estrella fine sandy loam (a sandy loam over yellow and red mottled clay over chalk) which is a savanna soil with its alternation of texture in the horizons. Another savanna soil at Camagüey is a brown clay over serpentine rock at only 2 to 8 in. depth, or else sandy loam over clay over serpentine at 5 to 18 in. The Holguin savanna has a red shallow clay over chalk. Typical savanna soil profiles of the South Plain of western Cuba were expressed diagrammatically by Bennett & Allison, from whose illustration Figure 15 has been adapted.

The savanna soil departs somewhat from this dominant pattern in the case of the Nipe clay soil of the Sierra de Nipe, already noted as the solitary case of savanna on mountain land. The Nipe soil consists of a friable red-brown clay filled with *perdigón* and about a foot deep overlying a horizon 5 to 6 ft. deep of deep red clay with *perdigón*, over, in turn, an orange friable clay with boulders of decomposition, reaching serpentine bed rock at a depth of some 16 ft. (Marbut 1932). This is a very peculiar soil of remarkable structure and composition: the internal drainage and chemistry of the profile are not clear. Presence of *perdigón* in the top horizon seems to indicate poor drainage.

Upland forest soils and swamp soils are both of distinct character from those of the savannas. The former are red, brown, yellow or grey but one does not remark the differentiation into textural horizons, nor the prominent occurrence of *perdigón* and *mocarrero*.

These are well drained soils both externally by reason of sloping topography and internally by virtue of a more or less freely draining profile. Swamp soils are generally dark colored, often black. The subsoil may or may not be impermeable but there is a permanently high water table due to low relief. "Hog-wallow" structure is a feature of these soils and a characteristic vegetation is often the Haematoxylon thicket. This tree is a thorny, microphyllous legume of stunted and gnarled growth (about 30 ft. in height at most) which when growing in a swampy habitat develops a much thickened base to the trunk with innumerable flutings or small buttresses. This community occurs also in Honduras.

In endeavoring to arrive at a generalization for the vegetation of the savannas it would appear that the two predominant grasses are *Sporobolus indicus* and *Andropogon virginicus*. Other grasses of more localized dominance mentioned by Marie-Victorin & León are *Sorghastrum stipoides*, *Arundinella deppeana*, *Panicum tenerum* and *Imperata brasiliensis*. Sedges are represented abundantly by *Rhynchospora globosa* and *Bulbostylis paradoxa*. Greatest variety seems to be lent to the savanna associations by changes in the arborescent components rather than in the herbs. One may naturally expect to hear of *Curatella americana*, *Byrsonima crassifolia*, and *B. verbascifolia*. Other small trees often found are *Brya ebenus*, *Rondeletia correifolia*, *Anacardium occidentale*, *Xylopia grandiflora* and *Tabebuia lepidophylla*. Such a chaparral, however, is not the predominant phase. Two different, very distinctive types are exceedingly well developed: the oak-pine type and the palm type. The Curatella-Byrsonima assemblage may be replaced by or mixed with Quercus and Pinus, single or together, or else the two latter may be replaced by groves of palmettoes of the genera *Sabal*, *Copernicia*, *Acoelorraphe* and *Colpothrinax*.

Pinnate palms (Roystonea, Acrocomia) are only rarely present. Most of the species of palmetto are endemic and some of them develop curious bulbous swellings on the trunk. They may occur in dense groves or as single, scattered individuals. All kinds of variations and combinations between *chaparral,* oak, pine and palmettoes are possible.

On the Holguin savanna in the east, where the soil is a clay over chalk, the aboreal element is said by Bennett & Allison to be a dense stand of *Sabal florida.* Much of this savanna, however, is on a shallow soil over serpentine rock, and the palms in this case are given by Seifriz as *Copernicia yarey* and *Coccothrinax garciana,* two species of smaller growth than the Sabal. The grasses *Andropogon virgatus, A. gracilis, Leptocoryphium lanatum, Sporobolus indicus* and *Panicum* spp. are noted as present, but the ground cover is said to be composed principally of "a rather dense growth of small shrubs, in part thorny" (Seifriz).

The Camagüey savannas, partly serpentine, partly sandy over clay, are of the palm type. Seifriz lists three species of Corpernicia and three of Coccothrinax, while Bennett & Allison mention *Sabal maritima, Byrsonima crassifolia* and *Sporobolus indicus.* The Santo Domingo savanna features the last three species without the Copernicia and Coccothrinax.

On the South Plain (*fide* Bennett & Allison) the vegetation associated with the typical soils of the rolling, well-drained region (see Fig. 15), is a savanna of *Sporobolus indicus* with Byrsonima, Sabal, and locally Roystonea and Colpothrinax. Sometimes this changes to Andropogon savanna with Byrsonima, Anacardium and pine. The savanna of the imperfectly drained flats is composed of *Andropogon virginicus* with a Paspalum and contains Colpothrinax, Copernicia and other palmettoes, *Byrsonima crassifolia* and *Malpighia glabra.*

Seifriz has given us a more complete list of the principal elements in the flora of this area, as follows: Palms are *Sabal florida, Colpothrinax wrightii, Copernicia glabrescens, Acoelorraphe wrightii.* Shrubs or small trees: *Byrsonima crassifolia, Rondeletia correifolia, Miconia delicatula, Tabebuia lepidophylla, Curatella americana, Vaccinium ramonii, Befaria cubensis* and *Kalmiella ericoides.* Grasses: *Paspalum pulchellum* and *P. plicatulum, Aristida refracta* and *A. neglecta, Cenchrus distichophyllus, Sporobolus*

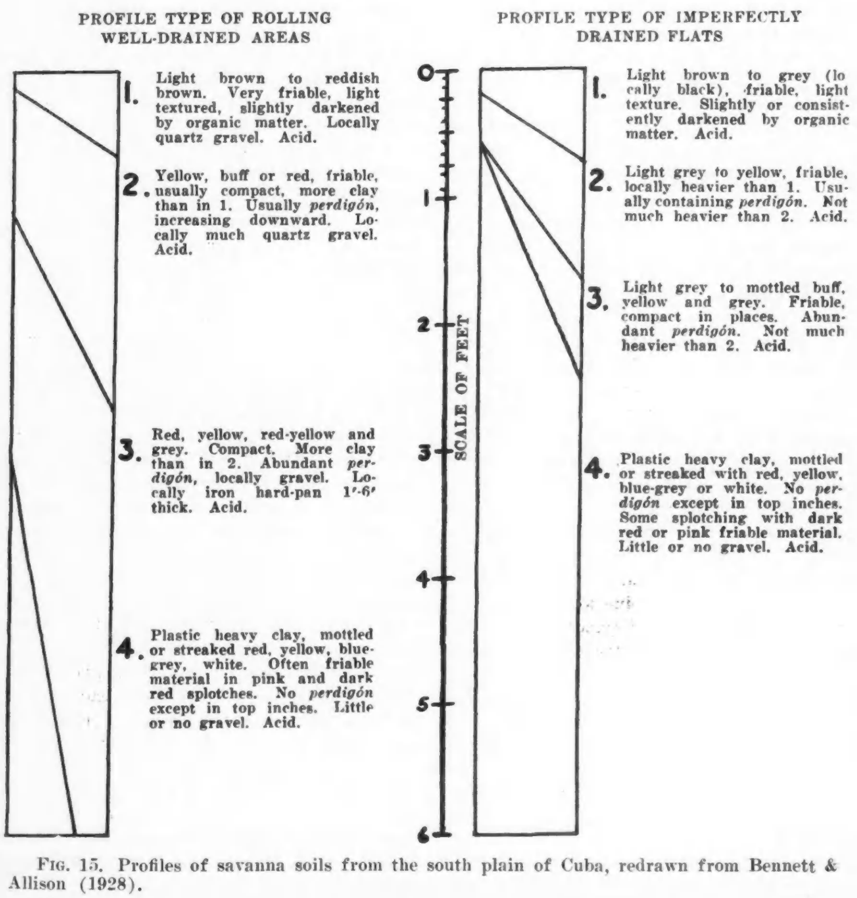

FIG. 15. Profiles of savanna soils from the south plain of Cuba, redrawn from Bennett & Allison (1928).

purpurascens, Andropogon virgatus and *A. virginicus, Panicum condensum, Trachypogon filifolius, Imperata brasiliensis.* Sedges: *Dichromena ciliata* and *Rhynchospora globosa.* Herbs are said to comprise numerous species of Xyridaceae, Eriocaulaceae, Droseraceae, Polygalaceae and Compositae.

Among the hills of the Sierra de los Organos Marie-Victorin & León encountered an association of *Quercus virginiana* and *Pinus tropicalis* in grassland of *Sorghastrum stipoides,* which they found to bear a striking resemblance to the *Quercus ilex-Pinus halepensis* association of the Mediterranean region, with this difference, that the other woody associates in the Mediterranean are microphyllous (Erica, Ulex) whereas those in Cuba have quite large leaves (Byrsonima, Rondeletia, Curatella). A variant of this association is *Quercus virginiana—Byrsonima crassifolia* over *Arundinella deppeana* with pine absent.

On the Isle of Pines the variations seem endless: "the appearance of the savannas changed unceasingly" wrote Marie-Victorin & León. Just a few of the types are:—*Sporobolus indicus* with Curatella, Tabebuia, Byrsonima, Brya and Rondeletia; *Imperata brasiliensis* and *Rhynchospora globosa* with Pinus and Colpothrinax; *Bulbostylis paradoxa* with Pinus and Tabebuia, or with Tabebuia alone or with Tabebuia and Rondeletia; *Rhynchospora globosa* with *Byrsonima verbascifolia.*

None of these variations in composition of the savannas has yet been studied in detail, and the reasons for them therefore are not yet understood. Clearly the variations are related to variations in soil moisture and drainage due to topography and soil structure.

The writer suggests that the palm savannas may be found to occupy the areas with clay or clayey topsoil and the orchard savannas the more sandy ground. Such floristic variations as occur do so, it will be observed, within rather narrow limits. There is a definite savanna flora which seldom mingles to any extent with forest elements. The Cuban savanna flora is closely related to that of other typical savannas of tropical America, but is remarkable in certain respects: it is very rich and it is very highly endemic. It seems probable that, if the plants of the Cuban savannas were completely catalogued, they would come near to equalling in number those found within any equivalent area of the Brazilian plateau, and would far outnumber the components of any other savannas north of the Amazon. The increased number of plants in Cuba is not due to the reappearance of Brazilian species of disjunct distribution which bypass Venezuela but to the many endemic species peculiar to the island. This high endemism is paralleled in the forest floras of the Greater Antilles also. Many of these endemic plants are also highly specialized, mostly with underground perennating organs which enable them to survive the fires. Among the most interesting of these are the species of the cycad genus Zamia, little plants with a bulbous underground stem.

Two further matters now remain to be considered: the vegetation of the Nipe plateau and that of the man-made grasslands.

For data on the Sierra de Nipe, we may refer to Carabia (1945). He described five vegetation types from the area, designated by their vernacular names. The *pinar* or pine savanna appears to be the most widespread, and next to it the *charrascal* or bushland. There is also *monte* or forest, mostly lower montane rain forest; *sabana,* mostly palm, savanna, and *sao,* a type of thorn scrub. The last named is associated with the dry habitat of the porous limestone *mogotes* and we need not be concerned with it. The remaining four communities occur upon soils developed to varying degrees from the same geological formation, serpentine. The *monte,* the forest, occurs on the most favorable sites "wherever the ground is not too steep and soil is deposited, enough to support a typical wet forest" (Carabia). The forest appears to occur, in fact, wherever a considerable depth of permeable, well-drained soil has developed above the serpentine rock and where the land is sloping. It occurs around the edges of the plateau, clearly where the soils are fairly young but developed to a reasonable depth. The forest appears from the description given to correspond to the formation lower montane rain forest and may be regarded as the climatic climax of the area.

The *charrascal,* on the other hand, occupies the least developed soils, shallow and rocky, where the serpentine has not decayed deeply. It varies from a rock-pavement vegetation of small, scattered shrubs to a "semi xerophytic community, formed mainly of woody shrubs and small trees 6 metres high or less, with stems 5-10 cm in diameter. The leaves are generally small and coriaceous, revolute, smooth, and lustrous on the upper part and with tomentum on the under surface." There seems little doubt that this corresponds essentially to the bushland of Barbuda.

The two savanna types, *sabana* proper and *pinar,* occupy in general the more highly weathered soils on the plateau, what Carabia calls "limonite soil" owing to the predominance of iron oxide. This is the Nipe clay of Marbut described above. The *sabana* is dominated by grasses and sedges, among which principally *Imperata brasiliensis* and *Leptocoryphium lanatum,* and typically it contains scattered palmettoes, *Copernicia yarey* and *Coccothrinax yuruguana.* According to Carabia, the presence of these latter in certain areas shows that they are true savannas. In other parts the *sabana* appears to have supplanted the *pinar,* the *charrascal* and the *monte* through burning.

Pinar occupies all the "limonite soils" between 400 and 600 m elevation. Grasses and sedges represent the true dominants of the *pinar* and forms a layer not much over 18 in. high. The actual dominant species are not stated but the list of components embraces seven species of *Panicum,* three each of *Andropogon* and *Laciasis,* two of *Paspalum, Imperata, Lithacne* and *Ichnanthus,* and *Leptocoryphium lanatum*: seven species of *Rhynchospora,* three of

Bulbostylis and two of *Scleria*. The list includes many typical savanna components. Several herbs and small woody subshrubs are also mentioned. The only tree is *Pinus cubensis*, reaching 50 to 80 ft. in height and 12-16 in. in diameter, the stems distributed 12 to 30 ft. apart.

Here and there in Cuba one has to deal with the effects of man's interference, and since the arrival of the European settler, many modifications have been brought about. As in Antigua, cattle-keeping has produced an entirely artificial type of grassland which has nothing in common with the natural savanna but resembles the grasslands of tropical Africa. Marie-Victorin & León observed: "In Africa the acacias are propagated by the great numbers of herbivorous animals: giraffes, antelopes, etc. There is a striking general analogy between the African savannas of the natural *Acacia-Andropogon* type and these Cuban savannas or pastures of the artificial *Samanea-Panicum* type. The same general appearance; the same complementary relation between a continuous stratum of Glumiflorae and an open formation of microphyllous leguminous trees; the same umbrella-shaped crowns of these trees, a form which seems to mark some height-ceiling. The general appearance of these two associations is the same, even if the genera and species which compose them are different."

In some other cases there is apparently a mixture of savanna with thorn bush or cactus. On the Trinidad plains, for example, Bennett & Allison describe a predominant savanna of Sporobolus with small trees of *Brya ebenus* and local thickets of *Copernicia macroglossa*, *Acacia farnesiana*, prickly pears and cacti. This intermixture seems to take the form of a mixture by patches rather than of an intimate mixture of the flora, and appears confined to the areas of lower rainfall.

CENTRAL AMERICA

BRITISH HONDURAS

Central America is a region of whose vegetation we know relatively little, ecologically. British Honduras is the only country in the region where the savannas have been studied in any detail. For the other countries we have only brief general accounts. The work of Charter (1941) in British Honduras is the only thorough study made of savanna vegetation in relation to soil and site in Central America and one of the best studies of the spbject to be made in all of the American tropics. The savannas are found on the lowlying parts of the country, principally on the northern plain, associated with soils developed on alluvial sands and clays deposited on top of the predominant limestones. Annual rainfall varies locally between 40 and 100 in. on the average, irregularly distributed, with generally four dry months in which less than 4 in. of rain falls. The limestones which underlie the bulk of the country are covered typically by a forest which appears to correspond

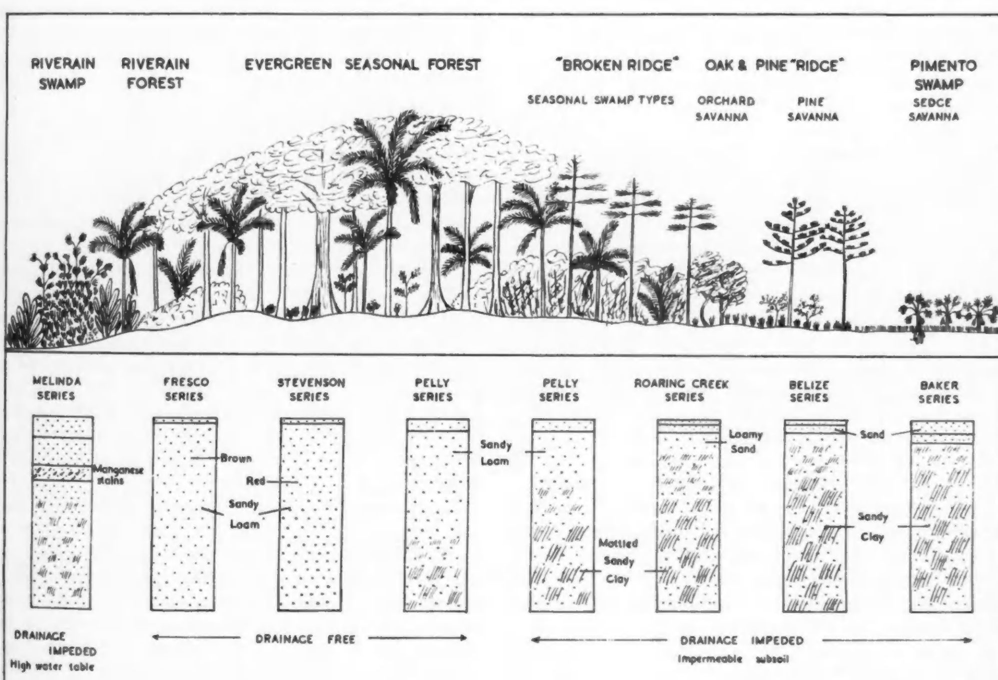

FIG. 16. Soil and Vegetation profiles from British Honduras. Redrawn from Charter (1941).

to the Semi-evergreen Seasonal Forest of Beard (1944), called "Quasi-rainforest" by Lundell (1945). Savannas do not occur on them. There is other forest on the mountains (? Lower Montane Rain Forest) and certain swamp types on flats. On the alluvial areas of the northern plain Charter described seven vegetation types, two of which are savanna. All of the seven are related to definite conditions of soil and site and were regarded by Charter as forming part of a developmental series. (See Fig. 16.) He suggested that the different soils of the area represented different stages of weathering and soil development, occurring on alluvial material of different age. The flattest areas forming terraces between the rivers would consist of the oldest material and show the most highly developed soil profiles, as indeed does appear to be the case. Nearer the rivers the parent material would be younger and the soil less developed. The following is an outline of Charter's description of this process.

Mixed alluvium derived from non-calcareous rocks is being deposited at the present day in the lower parts of the river valleys. The sites have a periodically high water-table and are subject to frequent flooding. The Melinda type of soil (Fig. 16) is developed, with a surface horizon of grey or grey-black loam overlying yellow-brown loam mottled grey and with manganese stains. The vegetation is riverain swamp with spiny bamboo (Guadua), Heliconia and palms.

With further development of the flood plain, the river cuts into the deposits it has laid down, the water table is lowered and flooding becomes less frequent. Products of drainage impedance thus disappear from the soil profile which becomes a uniformly yellow-brown loam (Fresco soil). A low riverain forest develops.

With the development of further relief and still better internal drainage, the soil undergoes more leaching and oxidation and becomes red or reddish-brown in color (Stevenson soil) carrying "high riverain rain forest." This is a more luxuriant forest than that found on the limestone areas of the Colony and probably corresponds to Beard's "Evergreen Seasonal Forest."

Later, obscure red and orange mottling develops at the base of the profile and the surface horizon assumes a greyish-brown tint. Gradually the upper humic layer becomes more pronounced, white mottling appears, and the lower part of the profile becomes an impermeable red and white mottled sandy clay (Pelly soil). Drainage impedance set up by the subsoil causes regression of the forest to a shorter, denser type, "broken ridge with cohune" (possibly Beard's Marsh Forest or Marsh Woodland).

With further aging of the soil material and with further increases in drainage impedance, the red and white mottled clay creeps higher up the profile (Roaring Creek Soil) and the woodland regresses still further to pure "broken ridge" (Marsh Woodland).

The impervious clays thus developed, apparently by illuviation of the lower layers, undergo further changes if they are of a sandy nature, due to sheet erosion. Surface water is now almost wholly removed by run-off and this carries with it clay to be deposited in depressions, leaving behind the sand. Eventually the mottled clay comes to be covered with a sandy layer a foot or more in depth. (Belize soil.) The vegetation changes over to savanna, at first with *Quercus* spp. ("oak ridge"), later with *Curatella americana* ("yaha") and *Byrsonima crassifolia* ("craboo"), when fully developed with pine (*Pinus caribaea*)—"pine ridge."

The final development of soil and site takes place with a levelling of the surface by sheet erosion. In the early stages, both internal and external drainage were good. Internal drainage gradually worsened and ceased as the subsoil became compacted. Now, on the flat expanses finally produced, external drainage ceases also and surplus water must be disposed of by evaporation. The Baker soils underlie level terraces flooded for long periods during the rainy season and completely dried out during the dry season. The vegetation is sedge savanna, expanses of sedgeland dotted over with clumps of the palm *Acoelorraphe wrightii* and isolated trees of *Crescentia cujete* and *Cameraria belizensis.*

A similar series of soil and vegetation types from mangrove swamp through high forest to pine and palm savanna was distinguished by Charter on the coastal plain.

"Mountain pine ridge" consists of areas of pine savanna in hilly areas over granodiorite intrusions. Charter showed this type to be associated with an impeded-drainage, sand-over-clay profile essentially similar in physical structure to the pine savanna soils of the plains.

OTHER CENTRAL AMERICAN COUNTRIES

Conditions typical of the low country of British Honduras are repeated in neighboring Guatemala and Yucatan. Standley & Steyermark (1945) described forests in the Petén province of Guatemala similar to those on the limestone areas of British Honduras, adding that "lakes, wooded swamps, undrained sinkhole ponds or aguadas, and stretches of grassland are scattered throughout, especially in central Petén, but in general the country is densely forested." The grasslands were further characterized as low savannas and said to consist of open stands of *Pinus caribaea, Curatella americana* and *Byrsonima crassifolia.* Evidently we have here the same mosaic of swamp, savanna and forest types as in British Honduras.

In the Republic of Honduras savannas with pine are found on hilly ground in the interior on sites probably similar to the "mountain pine ridge" of British Honduras and situated on geologically similar country. Treadwell, Hill & Bennett (1926) wrote that "much of the hill country of Honduras, in the western part at least, has a thin soil, often stony, on which there are extensive forests of pine. A considerable portion of this is covered with soil which will not average two feet in depth over bedrock (mainly

mica schist and light-colored volcanic rocks); often there is no soil covering at all." The rainfall here is said to average 30-60 in. a year, irregularly distributed with a severe dry season.

In the eastern part of Nicaragua, outside the young volcanic mountains, there appear to be savanna lands similar to the above, but we know little about them.

El Salvador contains savannas on the plains of the Pacific coast. According to Kovar (1945) "no small extent of arid and stony areas in the interior of the country are covered with *Curatella americana*, which at times grows associated with the "jícama," *Pachyrrhizus*." Other savannas on "plains with barren soil or badly drained in the rainy season" are characterized by the presence of *Crescentia alata*.

In Costa Rica and Panama savannas occur only on the drier Pacific side, the Atlantic slope being covered everywhere with heavy rain forest. On the Atlantic slope rainfall is in excess of 150 in. a year and there is no effective dry season. On the Pacific slope on the other hand precipitation is about half that of the Atlantic and is distributed with a severe dry season from January to April. Deciduous forests predominate on the Pacific side, interspersed with savanna areas. Of the latter, unfortunately, we know next to nothing.

THE GUIANA LOWLANDS

VENEZUELAN GUIANA

Guiana is, roughly, the region between the mouths of the Orinoco and Amazon rivers. Its heart consists of the Guiana shield, a highland massif of ancient rocks, and this is surrounded by lowlands which are in part reduced remnants of the same ancient core and in part land formed from the comparatively recent deposition of sediments on the continental foreland. The Venezuelan Guiana is of the former structure and it consists of the country immediately to the south of the Orinoco River and draining towards it. South of the Orinoco, therefore, the country is radically different in form from the flat plains of Pleistocene alluvium north of the river. It is developed upon a solid geology of hard metamorphic rocks and consists of gently undulating land, all less than 1,000 ft. above sea level, broken up with little hill ranges not exceeding 2,500 ft. in height. It is almost entirely savanna covered.

Between January 16th and 18th, 1945, the writer travelled by road from Ciudad Bolívar to Tumeremo via Upata, Guasipati and El Callao. Later, on February 8th, he crossed the same tract by plane at a low altitude and was enabled to get a general, bird's-eye view of conditions to add to the closer inspection made by road. From Ciudad Bolívar to Upata is 95 mi., from Upata to Guasipati 60, thence to El Callao 15 and finally from El Callao to Tumeremo 25 mi. The road leaves Ciudad Bolívar through country somewhat resembling the Mesa de Guanipa, gently undulating ground with a sandy topsoil and thickly grown with the usual gnarled savanna trees, called chaparral (Figure 17). *Curatella americana* is very abundant, other trees relatively rare. They include

FIG. 17. Typical savanna south of the Orinoco, near Upata, Venezuela. A light sandy topsoil ill-covered by the sparse grasses, and Curatella trees.

Byrsonima crassifolia, Bowdichia virgilioides and a thorn tree, possibly an Acacia. The small *Byrsonima verbascifolia* is occasionally seen. The ground is covered as usual with coarse bunch-grasses. On the flatter places, plateau sites rather than depressions, the tree growth thins out markedly, showing its sensitivity to drainage. The soil is sandy at the surface, littered with ironstone pebbles in varying quantity and of varying size. Some times the surface is quite thickly covered with gravel, in other places it is stoneless. All sizes of pebble are seen from that of a pea to that of a tennis ball. The sand horizon is yellowish to pale grey in color and changes abruptly at from one to two feet depth to a brilliant red, or red-white mottled, clay, extremely compact and hard. Small termite mounds like those of the Trinidad savannas are not uncommon. Rocky knolls disturb the general evenness of the savanna here and there and appear to be outcrops of some hard, igneous rock, possibly granite. These knolls consist for the most part of naked bosses of rock with a little thin chaparral in crevices. Sometimes, presumably when a reasonable depth of soil is present, the knolls bear a fair growth of deciduous seasonal forest, leafless at the time of the writer's journey. This same forest occurs in narrow strips along water courses where the principal trees are *Copaifera officinalis* L., *Bursera simaruba* (L.) Sarg. and *Cochlospermum vitifolium* Willd. Rarely, this streambank forest is replaced by thorn bush and often scattered Mauritia palms are present.

The road dips down gently to cross the Rio Caroní 78 km out of Ciudad Bolívar, with a magnificent view of range upon range of low hills beyond the river. The river itself is broad and sluggish and full of sand bars. Its level is subject to marked seasonal variation as the thickets of Annona and Pterocarpus lining its banks show, not only in the muddy marks of flood water on their trunks but in the adventitious root system which is put out at high level and left high and dry in the low season. Beyond the Caroní River to Upata the country is definitely hilly and is mainly covered with semi-evergreen seasonal forest, a slightly moister type than that seen further west. Savanna persists in a number of often rather unaccountable pockets, usually in the flatter places or where the soil is obviously shallow. Road cuttings

show the underlying rock to have decayed to very variable depths. Under forest, rock may not be encountered before 50 ft. depth, having weathered above to a red clay which turns brown in the surface horizon and is of good crumb structure. Roots penetrate deeply. Typically under savanna, rock is seen only 2 ft. below the surface and the ground is strewn besides with a layer of ironstone and quartzite pebbles. The brown clay topsoil below this merges at a foot depth into a red and white mottled zone which merges below into rotten rock. On such shallow sites there is equally poor drainage and little root-room as in the sand-over-clay soils, whereas on the very deep sites there is every opportunity for the development of forest growth. There does not, however, appear to be an invariable correlation here between the vegetation and the depth of soil. Leaving Upata on the road for Guasipati the hills are about half covered with savanna, half with forest and soil conditions could not be investigated. Savanna areas on flatter ground crossed by the road show a sand-over-clay type of soil for the most part, though outcrops of bosses of rock are frequent. The semi-evergreen forest contains *Copaifera officinalis* L., *Hymenaea courbaril* L. and *Genipa americana* L. Some miles further on, the road crosses a wide plain, very gently undulating and almost entirely covered with chaparral of Curatella, Bowdichia, Byrsonima and ?Acacia. The sand-over-clay soil is extremely quartzitic here and abundantly littered with quartz stones and boulders. Depressions and lines of drainage are occupied by dense thickets of Acacia, not the same species as occurs in the chaparral. Beyond this plain some hill ranges are crossed, their steep summits mainly clad with very open, almost treeless savanna. Deciduous seasonal forest occurs in a few haphazard patches on the slopes and at their feet together with some thorn thickets. Finally another plain, gently dissected, leads to Guasipati. Here there are actual ravines marked by occasional Mauritia palms instead of gentle depressions with thorn bush. Dense chaparral with Curatella dominant covers the lower ground while the tops of rises are almost bare and show dominance of *Byrsonima crassifolia*. These circumstances probably are due to a higher rainfall here.

El Callao nestles inside a range of low mountains which are unbrokenly covered with forest of semi-evergreen seasonal type. The savannas give place to forest midway between Guasipati and El Callao. The road from El Callao to Tumeremo is a very bad one and beginning in broken forested country is very muddy and difficult. When travelling on earth roads one appreciates an immediate difference between savanna and forest soils. The ground in savanna is compact, indurated and can be crossed even in wet weather. Forest ground is soft and loamy and readily forms into ruts and mudholes. After a mile or two, fortunately, the Tumeremo road emerges from the mountains and enters country of low relief consisting of a mass of little, gently rounded hillocks with depressions between them. This country is more settled than that previously crossed on the journey and carries more head of cattle. Consequently the vegetation has been somewhat disturbed and large areas consist of open pasture land or pasture with thorn bush. It seems that originally the little hills were covered with chaparral and the depressions with evergreen forest.

The forest grows more luxuriant and more evergreen steadily all the way from Ciudad Bolívar and one would expect a marked increase in rainfall. Actually the records show an average rainfall of only 55 in. per annum at Tumeremo which is still a low figure and cannot be more than 10 or 15 in. above that of Ciudad Bolívar. The average figures (courtesy of the Venezuelan Government) for the seven years 1938-1944 were:

Jan.	Feb.	Mar.	Apr.	May	June	July
86.1	60.4	66.5	84.4	157.1	191.7	188.5
3.6	2.5	2.7	3.5	6.5	8.0	7.9

Aug.	Sept.	Oct.	Nov.	Dec.	Total
159.9	50.7	94.1	85.9	101.3	1326.7 mm
6.7	2.1	3.9	3.5	4.2	55.2 in.

If these figures are correct one would not expect such a marked change in luxuriance of the forests seen along the route, but there are other factors at work such as the greater exposure to wind and lower humidity in predominantly grass-covered country.

From Tumeremo, making for the interior highlands, the journey was continued by plane to the southward and a month later the writer returned by plane all the way to Ciudad Bolívar. South of Tumeremo the country continues apparently somewhat flat for some little distance until the Cuyuni River is crossed, a wide, sluggish and meandering stream. Beyond the river the country rises in irregular mountain masses to the 6,000 ft. high Sierra de Lema which here marks the northern edge of the interior Guiana plateau. Immediately beyond the Sierra begins the open country of the Gran Sabana but the range itself and its foothills falling to and across the Cuyuni are covered with unbroken forest which appeared entirely evergreen from the air. This forest ceases at a definite line running in a north-east south-west direction between Tumeremo and the river. The writer did not have any opportunity to enter these forests nor to examine the nature of this forest boundary. It is possible that it marks the edge of the Cuyuni flood plain. On the Tumeremo side of the line the country takes on, from the air, a kind of checkerboard pattern: a mass of little, rounded rises (they are not worthy of the name "hills") covered with open savanna set in a matrix of evergreen for-

est which occupies the shallow depressions in between. The impression is not so much that of a dendritically arranged drainage system with forest along its channels and savanna on its watersheds as of a checkerboard system of small hillocks often almost circular in plan. From the air this is seen to remain the essential arrangement all the way to Ciudad Bolívar, a fact that is not so readily appreciated from the ground. Due apparently to gradually decreasing moisture along the line of flight the forest occupying the depressions and drainage channels is seen to change gradually from a tall evergreen type of Tumeremo to a low deciduous forest and finally to thorn scrub with a few Mauritia palms. Mountain ridges breaking out of the peneplain appear from the plane to be almost entirely forested with only occasional savanna patches on them, though exposures of absolutely bare rock are not uncommon.

Additional information on the Venezuelan Guiana is provided by Williams (1940, 1941). Along the lower Paragua savanna is the dominant formation. There are two main types, "fresh-water savannas" and "inland savannas," of which the latter is further divisible into two distinct communities. "Fresh-water savannas" correspond to the *esteros* of the llanos, depressions completely submerged in the rainy season. There are a number of small trees such as *Duroia sprucei* and *Erythrina glauca.* Herbaceous vegetation seems to be dominated by sedges, of which only *Rhynchospora globosa* is named. The "inland savannas" are situated beyond reach of seasonal floods upon a "well-drained sandy soil overlying marl beds." There are two divisions, treeless, and scattered with the usual Curatella-Byrsonima-Bowdichia shrubs. The exact composition of the grass association is not clear.

Along the Caura River, further west than the Paragua, there is a dominating distinction between savanna-covered plains and forested mountain country. The savannas appear to occupy flat terraces and conform to the usual floristic pattern with Curatella, Byrsonima, Bowdichia, etc. The soil is sandy or pebbly over a compacted sub-soil of quartz gravel.

Williams' observations reach as far as the upper Orinoco at the island of El Ratón above Puerto Ayacucho. In this region, he wrote, "it may be safely stated that the rainfall is much heavier in this territory and the dry season shorter than in the lower reaches of the Orinoco basin." At this point on the Orinoco the sedimentary llanos have been left behind and the savannas, stretching far away to the west of the river into Colombian territory, are interspersed with rounded, black (? granitic) rocks, some of them 200 or 300 ft. high.

The island of El Raton is traversed for almost its entire length north and south by a narrow savanna composed of *Bulbostylis junciformis, Scleria scabra, Trachypogon ligularis, Axonopus aureus, Panicum cervicatum* and *Clitoria simplicifolia,* as well as "a few low shrubs."

The headwaters of the Orinoco and its tributaries are said to be densely forested.

BRITISH, DUTCH AND FRENCH GUIANA

The lowland savanna country of the three European colonies in Guiana forms a definite unit and is quite a separate region from the Venezuelan Guiana savannas. The coastal region of the European colonies is low-lying and formed largely of Plio-Pleistocene alluvial deposits, mainly loose sands. The actual coastal belt is very swampy and contains large areas of mangrove, palm and herbaceous swamp vegetation. The open herbaceous swamps, filled with giant sedges and herbs such as *Cyperus giganteus* and *Montrichardia arborescens,* are referred to in British Guiana as "Savannahs," but this is not the legitimate use of the term. The true savannas occur on the slightly higher ground behind the coastal swamps, on the tops of the flat watersheds between the rivers and creeks, in the form of relatively small blocks and patches surrounded by forest, often by high rain forest. There is no broad belt of savanna country as in the Venezuelan Guiana. The region of these savannas begins in the east of British Guiana adjoining the Berbice River and continues eastward across Dutch and French Guiana to connect with similar country in Brazil about the Amazon mouths. There are no savannas between the Berbice-Demerara watershed and the Venezuelan frontier. A map showing the distribution of savanna country in British Guiana is given by Davis & Richards (1933, p. 354).

BRITISH GUIANA

Some of the savannas of the Berbice River district of British Guiana were described by Follett-Smith (1930) and Martyn (1931). The area surveyed covered some 70 sq. mi. of the Wiruni-Ituni savannas, about 60 mi. inland from the sea. The country consists of open undulating grassland 80-90 ft. above sea level, with scattered areas of forest varying in extent from several square miles to narrow belts of trees bordering creeks and streams. The savannas are covered by a thin, xerophytic vegetation which occupies no more than 60% of the surface of the soil and consists of a mixture of grasses and sedges. A feature of the open savanna country is the number of mounds raised by ants (*Atta* spp. according to Martyn, though Myers (1936) ascribed them mainly to Syntermes); "This subsoil, brought up by their activities, supports a flora apparently capable of withstanding the periodic savannah fires and resembles that found in the narrow transition zone between forest and open savannah country" (Follett-Smith). Other variations are the presence of water-holes, water-logged in the wet season, but dry during periods of drought, and the occurrence of slightly elevated and isolated areas of coarse white sand locally known as "muri" sand.

The average rainfall for the six years 1924-1929 at Ida Sabaina eleven miles from the area studied is shown in the following table. The rainfall of the savanna country is thought to be similar. Rainfall of this quantity and distribution is associated with country under high evergreen forest in Trinidad.

Jan.	Feb.	Mar.	Apr.	May	June	July
86.8	81.6	62.8	127.2	283.2	326.8	266.4
3.7	3.4	2.7	5.3	11.8	13.7	11.1

Aug.	Sept.	Oct.	Nov.	Dec.	Total
216.0	100.8	81.6	110.8	182.4	1934.4 mm
9.0	4.2	3.4	4.7	7.6	80.6 in.

Follett-Smith distinguished three main soil types—the brown sand type, the sand hill type and the muri sand type. The brown sand was found to be the most widespread. It consists of a fine brown sandy topsoil 10 in. deep over a subsoil slightly lighter in color merging at a depth of 2 ft. into a slightly heavier red brown loam. The soil is highly acidic throughout and organic matter content is low at the surface decreasing to negligible quantity below 10 in. The sand hill type of soil is a light to dark grey deep sand, occurring near to Waranama Creek. Muri sands occur on slight elevations and are usually accompanied by the presence of a waterhole. They consist of coarse white rounded grains of quartz. All of these soils are highly leached siliceous sands, permeable, acid in reaction and of low organic matter content. They are probably deficient in plant nutrients.

Martyn found that four species of grass and two of sedge were the chief constituents of the savanna vegetation which he termed the grass-sedge association. Composition was found to vary with soil type. On the sand hill soil the principal grasses were *Trachypogon plumosus* (H. & B.) Nees, *Axonopus aureus* Beauv., *Andropogon leucostachyus* HBK. and *Aristida setifolia* HBK., with *Leptocoryphium lanatum* (HBK.) Nees as a less common associate. *Trachypogon plumosus* was dominant, accounting for a quarter of the association. Sedges were represented principally by *Rhynchospora pterocarpa* R. & S., with *Stenophyllus coniferus* (Kunth.) Britton appearing as tufts in bare patches of soil. On the brown soil type the vegetation is thinner, sedges are more prevalent, and Andropogon and Aristida are less frequent.

Stunted bushes of *Byrsonima coccolobaefolia* and *Curatella americana* occur here and there, becoming a "dominant feature" in certain areas. The recumbent woody *Pavonia speciosa, Palicourea rigida* and *Byrsonima verbascifolia* are seen throughout.

Scattered across the savannas at intervals are shallow depressions called "pans" which seem analogous to the *esteros* of the llanos and *baixas* of the interior. They are under water in the rainy seeason, dry during drought.

The muri sands do not carry savanna at all, but a distinct, woody plant association, markedly xerophytic in character. This consists of thick patches of bushes and small trees, interspersed with open areas on which the vegetation is of a very sparse nature. *Clusia nemorosa* is usually the largest component of the scrub and arises in the centre of the thickets, attaining a height of fifteen to twenty feet. It is sometimes accompanied by stunted trees of *Byrsonima spicata.* A shrub, *Pagamea capitata*, normally some 6 ft. high, and the low-growing "muri bush," *Humirium floribundum* var. *guianense*, make up the remainder of the thickets.

The open areas of the muri bush are sparsely occupied by *Cassia uniflora* and clumps of "muri grass," *Axonopus attenuatus*, together with *Cryptangium uliginosum* and scattered shoots of *Trachypogon plumosus.* Small patches of the fern *Schizea incurvata* are always present and two species of Borreria.

Transition to forest at the borders of the savannas is abrupt and there is only a narrow transition zone. No details of the structure or composition of this forest are available. Martyn described, however, the plants of the transition zone, which he found repeated, in a rather interesting manner, on the ant hills in the savanna itself. A definite series of communities intermediate between savanna and "transitional bush" can be traced. In the first stage there is merely a richer herbaceous vegetation: two new sedges appear, *Rhynchospora cephalotes* and *Dichromena ciliata. Sipanea pratensis* and *Tibouchina aspera* are conspicuous. In the next stage, *R. cephalotes* attains greater prominence and several species of *Miconia* including *M. macrothyrsa* are found, with seedlings of *Byrsonima spicata* and bushes of *Siparuna guianensis* and *Eugenia benthamii.* In the third and final stage a little island of bushes is formed, surmounted by one or two trees. *Byrsonima spicata* is dominant accompanied by *Miconia rubiginosa, Solanum asperum* and *Wulffia baccata* among others. Martyn tentatively attributed this phenomenon to immunity from fire conferred by elevation upon the ant mounds. These savannas are frequently burned over but the fires never appear to penetrate the surrounding forest.

DUTCH GUIANA (SURINAM)

One of the best analyses of the savanna question that has been written in South America, together with some very clear descriptive matter on the lowland savannas of Surinam is that of Lanjouw (1936).

These savannas are found principally in the coastal region of the country, in the zone of continental alluvia adjoining the fluvio-marine deposits inland. Their surface is gently undulating and they occupy plateau sites on the watersheds between the rivers and creeks in the form of small blocks and patches surrounded by forest, very much as the savannas in Trinidad do. The exact nature of the soil was not made very clear by Lanjouw who quoted a work by Ijzerman (1931): "the sharp and coarse quartz sand found on the surface is typical of the savannahs: by the side of this sand, sandy clays occupy no insignificant part and both may occur in the same sa-

vannah." Ijzerman evidently considered both soil and subsoil to be readily permeable as he accounted for the presence of the savannas on the ground of impoverishment of the soil by leaching. One interesting fact brought out is that "it should be expressly pointed out that the profile of the subsoil in the savannahs shows no difference from that which characterizes the continental alluvia elsewhere; borings made in the savannahs and in the neighboring forest indicate this clearly."

The rainfall of the savanna region is given for three stations in the vicinity, Republiek, Sectie O, and Brownsweg, the average precipitation being 86.2, 85.7 and 92.5 in. per annum respectively. This rainfall regime shows a double seasonal fluctuation with two maxima and two minima, but the dry seasons are short and mild. The figures do not differ much from those for the Berbice savannas, the chief difference being that the second dry season is here sharper than the first. These savannas are subject to frequent fires.

Lanjouw wrote: "The general aspect of the Suriname savannahs is a slightly rolling landscape for the greater part covered with herbs, most of them with a more or less xeromorph habit or with a short and rapid vegetation period, and here and there some shrubs, or low and often deformed trees. An important part of this vegetation is occupied by the *Cyperaceae*, while in most places the *Gramineae* come on the second plan, though there are savannahs where the *Gramineae* are dominant. The dominance of the species changes often on short distances and in many places sharp lines can be drawn between the "associations." I have noticed that nearly always one can assign 1 or 2 species which are dominant." Most of the herbs and shrubs are said to flower at the end of the major rainy season, that is, in August.

Details of composition show several different types of savanna communities. There are two broad divisions, "wet" and "dry" savannas, the terms being relative only. In the former *Lagenocarpus tremulus* Nees is the dominant, with several species of *Rhynchospora*, a *Utricularia*, a *Drosera*, a *Lycopodium* and several herbs of the Xyridaceae and Eriocaulaceae. Grasses are rare to absent. Some fifteen species of shrubs and small trees are mentioned, but from the photographs these appear to be few, small and scattered. The vegetation does not cover more than 20%-40% of the soil, which several of the photographs (even one of "dry" savanna) show to be covered with standing water. Lanjouw mentions one "wet" savanna as being covered with 5 cm of water at the end of July. This is against the leaching theory of Ijzerman: evidently the soil is not at all permeable, at least in parts. Parts of the savannas are said to be inundated and to carry groves of *Mauritia flexuosa* L.f.

On the "dry" savannas Rhynchosporas may be dominant, but generally grasses, either *Trachypogon plumosus* or *Gymnopogon foliosus* Nees. The shrubs may often be taller and more abundant.

The forest surrounding these savannas is evidently often of a somewhat specialized type and is referred to by Lanjouw as "Savannah Forest," but unfortunately it is not described and it is difficult to gain an idea of the tree composition from the list of species. It is said to be less dense than the rain forest and to have a different, more or less xerophytic vegetation in the undergrowth.

Lanjouw's very interesting theory of the origin of these savannas has been outlined in the introduction to this paper.

Ijzerman (quoted by Lanjouw) wrote "Parts that seem destined later on to give rise to savannahs may also be met within the forests. The soil there has the same character as in the savannahs and the trees . . . are greatly stunted in growth. Such like forests are known in Surinam under the name of "Moeri-moeri-bosch," and, in so far as they are not caused by solid rock lying close to the surface, they are produced by the same factor as the savannahs." Stahel (1936) gave some notes on this moeri-moeri bush (translation). "Before the line reaches this creek it crosses an area which the woodsmen call 'moeri-moeri.' Here the granite rocks either come quite to the surface or are only covered with a thin layer of soil. This formation, the moeri-moeri, I very often met in the Surinam forests, generally only in small patches. These are covered with low shrubs and small trees, and only on the parts with rather more soil are there any large trees, which notably include many species with latex. The "bolletrie" (*Manilkara bidentata*) is chiefly sought for in moeri-moeri, as is well known to the balata bleeders. Wherever the rock pavements are not covered with humus, large bromeliads grow with Aroids and Orchids."

In the latter case the moeri-moeri seems to be a low evergreen scrub such as one would expect to find on rock pavements. If, as according to Ijzerman it is also found on deeper ground, then this presumably consists of reefs of white sand as in British Guiana. In neither case is it easy to understand how Ijzerman and Lanjouw can consider the soil as intermediate between that of forest and savanna.

FRENCH GUIANA

The topography of French Guiana is similar to that of all this region; a low-lying swampy coast rising gently inland, the higher interior being formed of ancient continental rocks and the coastal lands of alluvial deposits. According to Benoist (1924) the annual rainfall on the coast amounts to some 3.50 m, that is, 140 in., well distributed throughout the year with only a mild "dry season" often of no more than a few weeks duration between July and September. Humidity is high and variations in temperature slight. We may, therefore, expect to find that the bulk of the country is covered with high rain forest and in Benoist's account this is said to extend over 7/8ths of the area. Benoist distinguished two other botanical regions: a littoral zone of tidal mudflats and sea-sands, covered with mangroves and so on, and an intermediate belt some 10 to 15 mi. wide between the littoral and the rain forest which

is covered with savannas. These are described as sometimes dry, sometimes swampy, broken up by clumps of woodland or scattered over with isolated trees. As in British Guiana, the term "savane" is said to have a wide application locally and be extended even to everything which is not forest. For the most part, however, the "savanes" of French Guiana are true savannas and correspond very closely to those of Surinam in composition and habitat. Just as the Surinam savannas were divided by Lanjouw into "wet" and "dry," those of French Guiana were divided by Benoist into "wet," "intermediate" and "dry," of which the last two correspond closely to the "wet" of Surinam, Benoist's wet savannas being equivalent to the wet savannas of British Guiana and correctly herbaceous swamps, not savannas at all. They are perpetually inundated and filled with giant herbs such as Montrichardia, many tall Cyperaceae and water-loving grasses such as Leersia.

The dry savannas are described as relatively large, undulating expanses, abruptly bordered by high forest. There may or may not be shrubs and small trees present. The nature of the soil is not stated: it is only clear that these savannas occupy alluvial terraces and become very dry in the short dry season. The herbage dies down at this stage and it is generally burned off in September or October where fresh pasturage is required for cattle. Maximum vegetative activity occurs in May, followed by the flowering season in June. The herbaceous cover consists of both small sedges and bunch-grasses, the former predominant. No list of the Cyperaceae is given by Benoist but the principal grasses are said to be *Aristida tincta* Tr., *Trachypogon plumosus*, *Axonopus scoparius* Hitchc., and *Panicum cyanescens* Nees. There are also many dicotyledonous herbs, the recumbent shrub *Byrsonima verbascifolia* is locally abundant, and where there are taller shrubs and small trees they are *Curatella americana* L., *Byrsonima crassifolia* and *Palicourea rigida* HBK. The palm *Mauritia flexuosa* L. is found along streams.

The "intermediate" savannas lie nearer to the coast on lower ground, are wetter in the rainy season being sometimes actually under water, and less completely dry in the dry season. They are smaller and frequently consist of quite small patches set in the midst of forest, or of a maze of small glades: as Benoist puts it in one case, forming "a veritable labyrinth." Sedges here are completely dominant, numbering *Rhynchospora pterocarpa* R. & S. and several other Rhynchospora species, *Lagenocarpus tremulus* Nees, two species of *Scleria* and *Bulbostylis capillaris* Clarke. The less numerous grasses include *Echinolaena inflexa* Chase, *Panicum cyanescens* Nees, *Aristida tincta*, and *Andropogon leucostachyus*. Small flowering herbs are plentiful, including *Utriculariaceae*. Trees and shrubs are smaller, Curatella disappears, giving way to *Chrysobalanus pellocarpus* and smaller shrubs such as *Cassia uniflora* and *Tibouchina aspera*. The larger woody plants are usually loaded with epiphytic bromeliads. In the marshier places, *Mauritia flexuosa* becomes very abundant. The resemblance between these and the Aripo savannas of Trinidad is very close.

Benoist considered that the savannas of French Guiana must be due to man, who has cut down the forest in shifting cultivation, subsequently burning and pasturing the regrowth. He cited cases where pastures for stock have originated in this way from forest, though their flora was admitted to be quite different from that of the natural savannas.

THE GUIANA HIGHLANDS

LA GRAN SABANA

In the south-eastern corner of Venezuela lies the great, grass-covered plateau known as La Gran Sabana—the grand savanna. This region is some 150 miles square, in the angle formed by the Venezuela-British Guiana and Venezuela-Brazil frontiers. It is bounded on the north by the 6,000 ft. Sierra de Lema, a forest covered range forming the edge of the Guiana plateau and described in the section on the Venezuelan Guiana. On the south the Gran Sabana is bounded by the ill-defined Sierra de Pakaraima, the watershed between the Amazon and Orinoco basins, which is also the line of the Brazilian border and is partly forest covered. On the east and west the Sabana is limited by systems of huge sandstone mesas typical of which is the world-famous Mount Roraima, 9,300 ft. high (Fig. 18).

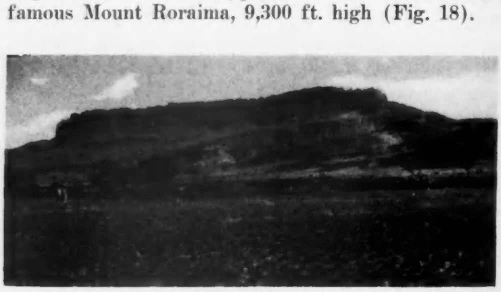

FIG. 18. Mount Roraima from the south. In the foreground are a few trees and bushes along a stream and the rest is open country.

The Gran Sabana itself is a plateau 3,000 to 4,000 ft. above sea level formed for the most part of horizontal sandstone strata of the Kaieteurean formation with basic igneous intrusions. It drains towards the south and south-west, all streams being caught in the south-west corner by the Rio Caroní which turns north to join the Orinoco. The Sabana is by no means an even, level plateau for the vertical block formation of the great mesas is continued in miniature down to the smallest features and the plateau is a disordered arrangement of flat-topped mesetas, benches and terraces bounded by scarp faces, a grand design of horizontal and vertical planes. Rounded country is only seen in the extreme south in and close to the Sierra de Pakaraima where the Kaieteurean rocks give way to the ancient igneous and metamorphic rocks of the basement complex. The streams draining the Gran Sabana flow in sluggish

stretches across great levels, swinging in prodigious meanders, until they drop suddenly in a spectacular waterfall over an escarpment and resume their slow meandering across another level stretch below until another waterfall is reached. The Gran Sabana landscape is, therefore, compounded of three features: broad and swampy river flats, wide, upland plateau levels and very steeply sloping scarp faces joining these two. Small rounded knolls are a minor feature.

The vegetation of the Gran Sabana consists for the most part of an absolutely treeless, open grassland, the chaparral of lowland Guiana being quite absent (Fig. 19). The writer did not see *Curatella americana* or *Bowdichia virgilioides* anywhere on the Sabana and *Byrsonima crassifolia* is rare. The herbaceous vegetation consists of bunch grasses and small sedges. The grasses are dominant in the sense of physical superiority as they outgrow and overshade the sedges at the time of most luxuriant growth, but the sedges are frequently present in equal numbers.

FIG. 19. General aspect of the Gran Sabana with *Uei tepui* in the background. Patches of forest are seen following streams or nestling into escarpment valleys. The savanna is treeless on the higher ground but becomes sparsely dotted with *Byrsonima crassifolia* in the hollow.

FIG. 20. Mauritia palms decking the swampy savanna of the flat Kukenan valley.

One of the commonest sedges is one which forms a short thick trunk up to 6 in. high with a rosette of leaves and inflorescences on top (Figs. 25-29). In addition to the open grassland there are lesser areas of morichal, scrub and forest. The morichales occur in the swampier parts of the river flats and consist of open stands of Mauritia palms with a sedge undergrowth (Fig. 20). Low woody scrub is found on beds of deep, white sand which occur rather rarely (Fig. 21). Forest occurs as gallery forest along the river banks and as rather odd pockets on many of the steep scarp slopes, usually nestling into a hollow. Its distribution in the latter cases is very irregular and inconsistent.

FIG. 21. "Muri bush" on a reef of deep sand, in the midst of open savanna.

The Gran Sabana has recently been thoroughly explored by the Venezuelan Government and a report published (Aguerrevere y otros, 1939), describing the geomorphology, geology, minerology and soils.

The rainfall at Santa Elena on the Sabana for the 5 years 1940-1944 (courtesy of the Venezuelan Government) showed the following averages:

Jan.	Feb.	Mar.	Apr.	May	June	July
51.7	37.0	96.6	122.0	184.8	266.5	198.7
2.2	1.5	4.0	5.1	7.7	11.1	8.3

Aug.	Sept.	Oct.	Nov.	Dec.	Total
185.2	111.5	85.5	145.8	145.9	1631.4 mm
7.7	4.6	3.5	6.1	6.1	67.9 in.

This rainfall and its distribution is closely similar to that obtaining over a large part of Trinidad where the vegetation is an evergreen seasonal forest.

In the last decade the discovery of diamond workings and the development of air transport has encouraged the much greater accessibility of this formerly very remote region and there is now a regular plane service from Ciudad Bolívar and Tumeremo to Santa Elena de Uairén on the southern edge of the Gran Sabana. The writer travelled by this route to Santa Elena on January 19th, 1945, accompanied by his wife and Mr. Alan Jones, Zoologist, and after staying a few days in Santa Elena left on foot for Mount Roraima on January 24th. The summit of Roraima was reached on January 30th travelling by the direct route up the Rio Kukenán, and the more circuitous route by Arabopó was taken for the return journey to Santa Elena, reached on February 5th. The party left Santa Elena by air for Ciudad Bolívar on February 8th. This journey was assisted by the Venezuelan Government to whom thanks are rendered. The observations which follow are being published for the first time.

Roraima lies fifty air-line miles to the north-east of Santa Elena across typical country of the Gran Sabana. The writer was unfortunately unable to collect any plants for identification but information on the grasses is taken from Myers' paper (1936). Santa Elena is a small village set in a valley among hills forming the outskirts of the Sierra de Pakaraima. The track towards Roraima follows the valley of the Rio Uairén, flowing northwards, to its junction with the Rio Kukenán which comes down from Roraima itself. The valley of the Uairén is broad and flat and the river meanders widely. It is bordered by lines of hills forming escarpments in an east-west direction, that is, at right angles to the line of the river. The rocks here are quartzites forming part of the basement complex and they dip towards the north. The steep scarp faces are rocky and covered with a sparse grass vegetation but the dip slopes are capped with loose white sand of unknown depth and bear a low open, woody scrub with very little grass. This consists of low trees, less than 10 ft. high, with small, hard leaves, evergreen and with ground plants containing a bracken fern and a number of terrestrial orchids. The general appearance is suggestive of the vegetation of coastal sand dunes, or of the "muri" scrub of lowland Guiana and this vegetation is undoubtedly related to similar scrub noted by Myers (1936) *in the midst of forest* south-east of Roraima. The Rio Uairén is bordered by tall evergreen gallery forest and the valley floor outside the forest is open grass with occasional morichales.

On reaching the Rio Kukenán one is properly on the Gran Sabana, on the Kaieteurean rocks whose horizontal strata form the steep and cliff-like walls of the valley. The valley floor is wide and flat, evidently filled with alluvial material. The river meanders very markedly and is bordered by a narrow belt of gallery forest, the remainder of the valley being about two thirds open grassland one third morichal. At the time of the writer's visit most of the valley bottom was firm and dry but it is evidently somewhat swampy in the rainy season. The morichales occupy the swampiest portions: frequently depressions which are clearly occluded meanders of the river. The ground surface is frequently hog-wallowed in and around morichales but this phenomenon is not otherwise observed on the Gran Sabana. The soil at Divina Pastora on the Kukenán flat was seen to be a blackish loam merging at 3 ft. depth into a grey loam, which merges at 6 ft. into a reddish loam and this at still greater depth leads to a red-mottled sand or clay. This is a deep soil without impedance, but presumably it has a seasonally high water-table due to low relief.

Large termite mounds are a prominent feature of these alluvial sites. They are not found on residual soils, in forest or in morichales but only on the drier alluvial savanna-covered soils where they are invariably present in large numbers. The large conical termitaria of Amitermes mentioned by Myers (1936) on the Rupununi savannas were not seen by the writer on the Gran Sabana, only the low, wide mounds of the type ascribed by Myers to a Syntermes. These mounds measure commonly from 6 to 12 ft. in diameter and from 1 to 3 ft. in height, in the shape of a gently raised dome. The largest mound seen by the writer measured 40 ft. by 27 and was 6 ft. in height, but such a size is exceptional. The mounds are often surprisingly regularly spaced, being distributed at approximately 30 ft. centres with almost mathematical regularity (Fig. 22). They carry a characteristic grass vegetation (Myers 1936, p. 179) but no woody plants.

Fig. 22. Termitaria on an alluvial flat along the Arabopó River. (Photo by Allan Jones.)

From the junction of the Uairén and Kukenán rivers, the route lies up the right bank of the Kukenán all the way to Roraima, first north-east to the Morock Falls and the junction of the Arabopó River, thence due northwards. The valley up to the Morock Falls is broad and flat with abrupt scarp-faces set well back. Tall, evergreen gallery forest borders the meandering Kukenán and there are substantial patches of forest surrounding the headwaters of most tributaries, clustering into the valley walls. In nearly every case these forests give place to morichales along the streams when these reach the valley floor and they are not, therefore, continuous with the gallery forests. The forests of the slopes nearly always give the impression of nestling into some protective cranny in the hills. The valley floor outside the gallery forest is as usual divided between dry grassland (*Sporobolus indicus*) with termite mounds and morichales. The hill-slopes, where not forested, are exceedingly bare and covered with such a thin growth of grass that the red color of the soil shows through, and is visible for miles. Even the soil-covering itself is thin and the nature and strike of the rock strata can often be readily seen. The waterfall Luei Meru is passed on the way to Morock Meru, formed by descent of a tributary stream into the valley. Some areas of white sand occur close to the fall and are covered with the usual "muri" scrub. The rocky walls of the gorge are tree covered.

Above Morock Meru the Kukenán valley is higher and narrower but the river still swings in sluggish meanders between small sudden descents at rapids and waterfalls. Morichales gradually disappear altogether. One begins, however, to encounter much larger and better developed patches of hill forest on

the sides of streams coming down from the hills. There is no difference in type between the gallery and hill forests anywhere along the writer's route and they belong to a formation not hitherto seen elsewhere. It should probably be classed as "dry evergreen." In the height of the dry season, no deciduous trees were seen and evergreens with hard leaves predominate. The forest is not tall, about 80 ft. in height at most, and composed of crowded, rather slender stems with a general maximum girth of 3 to 4 ft. There is a closed upper canopy and a small tree layer below. The palm *Jessenia oligocarpa* Gr. & Wendl. is rather abundant and reaches the canopy layer. Trees noted include:

Simaruba amara Aubl.	*Didymopanax morototoni* (Aubl.) Dcne & Pl.
Buchenavia capitata (Vahl.) Eichl.	*Tabebuia* sp.
Symphonia globulifera L.f.	*Clusia* sp.
Toromita sp.	*Rudgea* sp.
Vismia spp.	
Myrtaceae and Melastomaceae spp.	*Bactris* sp.

The boundary of a patch of forest is generally a ravine or a sudden break in the ground, the crest of a ridge or edge of a declivity. Boundaries are usually sharp and not marked by a transitional zone save rarely when a species of bamboo may form small thickets between the forest and the savanna.

Eight miles above Morock Meru, about 35 mi. from Santa Elena, the trail passes through the first Indian village seen on the way. It consists of two huts only. In the last generation these people, who are of the Arecuna tribe, have been brought into some contact with civilization through the visits of explorers and missionaries and are now familiar with the uses of clothing and firearms and certain other civilized equipment but their ways of life remain as yet unchanged. They live by cultivating small provision patches, chiefly for cassava, in the forest lands (they do not cultivate the savanna) and supplement this vegetable diet with such wild animal food, including insects, as they are able to catch. They have no domestic animals, and there is no native fauna of grazing animals on the grasslands of South America. Such animals as the Indians have available for hunting are forest animals—deer, wild pig, agouti, capybara, monkeys and birds—which are quite rare in this region. In this particular district the fish in the rivers are at most 6 in. in length. Meat diet for the aborigines is thus very scanty and is said to be augmented with termites and other insects. The termites and the "ant eaters" which prey upon them are in fact almost the only legitimate savanna fauna in South America.

Only two other aboriginal villages were seen on the Roraima expedition: Kunu-tá, about 8 mi. north-east of the two huts mentioned above, with about 10 houses and Arabopó, 5 mi. east of Roraima, which is only inhabited today by one family. An abandoned site was seen between Kunu-ta and Roraima which is probably the Kamaiwawong of the earlier explorers. The aboriginal population is thus extremely small, perhaps averaging one person per 10 sq. mi. None the less they manage very thoroughly to set fire to the savannas every year. Grass seems to be regularly fired as soon as it gets long enough and full of enough dead trash to burn. These savannas are swept by strong breezes and dead grass dries rapidly after rain so that a fire can be set at almost any time though of course the dry season provides best conditions. The writer's three Indian carriers, on being allowed to have matches, set fire to the grass along the trail several times a day, whenever a patch of tall grass was crossed. When questioned they were unable to give any coherent reason for their actions. It is probable that basically the desire is to keep the country open. Other wandering Indians were evidently doing likewise for columns of smoke were often seen and later, from the camp site on Roraima overlooking the Gran Sabana, many grass fires could be seen blazing at night.

Nearing the base of Roraima, many of the patches of forest are seen to have been overrun by fire and are now fringed by dead trees or even consist entirely of groves of blackened trunks (Fig. 23). The sloping base of Roraima itself between the foot of the great vertical cliff and the level of the savannas, has been forested in the recent past and the base of its neighbor Kukenán-tepui is still covered with evergreen forest. Fire passed across the slopes of Roraima, perhaps in the drought of 1926, and killed the trees for miles. They still stand there, dead, their trunks blackened by subsequent fires, over a low understory of bracken and small bushes (Fig. 24). Relics show that there was formerly a succession of montane vegetation-types on the mountain, due to increasing altitude and higher rainfall attracted by the massif. The general dry evergreen forest of the Gran Sabana gave place to lower montane and montane rain forests and finally to elfin woodland at 7,000 ft. close up under the cliff-foot. A certain amount of the latter has escaped the fire and is seen to contain characteristically an Oreopanax, Weinmannia and Hedyosmum, a large, stout, Geonoma

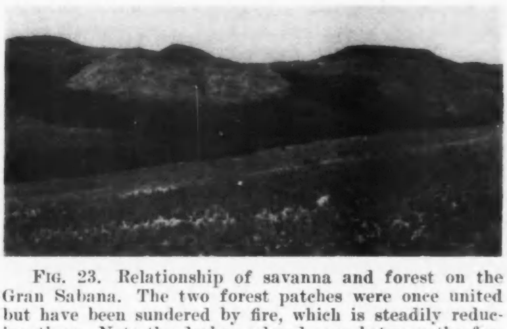

FIG. 23. Relationship of savanna and forest on the Gran Sabana. The two forest patches were once united but have been sundered by fire, which is steadily reducing them. Note the darker colored area between the forest patches which consists of low bush and bracken recently burnt over, and the dead trees at the forest borders.

FIG. 24. The dead forest on the slopes of Roraima.

palm and a small Euterpe. Mosses and epiphytes are much in evidence. The actual summit of Roraima supports a type of wet *páramo* vegetation growing in peat bog.

After coming down from Roraima a trail was followed eastwards to Arabopó village on the headwaters of the river of that name which unites with the Kukenán below Morock Meru. Arabopó lies between Roraima and Uei-tepui, the watershed linking these two mesas marking the line of the Brazilian frontier. Beyond Arabopó and stretching over into Brazil and beyond to British Guiana is solidly forested country, its border with the Gran Sabana marked by broad belts of dead trees killed by the same fire that exterminated the Roraima forest. One leaves the country of scarp and flat for an undulating landscape of ridge and valley in crossing over to the forest country, also the rainfall appears to be higher in that direction (the north east) judging by a comparison of cloud formations that way and over the Sabana at this particular season. To the northeast there was a thicker and more persistent cloud formation, suggesting a higher and more persistent rainfall. The same appears to be true of the Sierra de Lema on the north of the Gran Sabana. It would be natural to find that mountainous country rising up to the interior plateau on its windward side would catch a heavy rainfall and that plateau itself was somewhat drier.

The first few miles of the return journey from Arabopó follow the river downstream and pass through the tension belt between forest and savanna. The uplands to the west of the river are in pure grass, to the east in dense forest. The escarpment above the west bank has been covered with forest, which has suffered severely from fire and now consists of groves of dead trees or small bush or bracken. On the east bank there are many irregular patches of savanna set in forest mostly either in the river flat or on ridge tops and little plateau sites. There is a quantity of dead forest also. Five miles downstream from Arabopó the trail crosses the river and leads up onto the plateau between the Arabopó and Kukenán rivers, crossing over to join the trail of the up-journey above Morock Meru. This plateau is relatively even on top and entirely open, affording magnificent views in every direction, limited on the north and east by the great mesas. It is formed by a series of vast, sweeping levels, bordered by long flat ridges or by small rounded knolls and draining off at the sides into ravines which plunge suddenly to the valleys. The land is utterly treeless, stretching away for miles without so much as a shrub in sight, a monotonous carpet of grey grass broken on the flats by rows of termite heaps. A strong breeze is continually blowing and at this altitude (about 4,000 ft.) is pleasantly cool, though the sun's rays are fierce.

There are two principal types of site on the savannas which may be termed the alluvial and the residual and are repeated both in the valleys and on the uplands. The alluvial sites are flat and lie below some other feature such as a knoll or escarpment. They appear to have been formed by deposition of fine alluvial matter washed from above and laid down probably in fine sheets. The vegetation consists of coarse grass in scattered clumps (*Trachypogon plumosus* on the Uplands, *Sporobolus indicus* on the river flats), and sedges, particularly the little trunk-forming species (? *Bulbostylis paradoxa*). Termite mounds are almost invariably associated with these alluvial sites (Fig. 25). The soil is a greyish-white silty clay, stoneless and merging below a depth of 2 to 3 ft. into a pink and white mottled silty clay. It is non-cracking and quite extraordinarily hard and compact. With only a spade at one's disposal it was practically impossible to dig the ground and a couple of termitaria were only taken to pieces with the greatest labor. Admittedly this was the dry season but several rainy days occurred during the writer's journey to Roraima and the rain was quite without effect. There seemed to be no absorption by the soil. During rain, water collected in pools and began to stream off laterally in little clear rivulets. After two days of intermittent rain, moisture had not penetrated the soil for more than $\frac{1}{4}$ in. and after a day's sunshine this top layer had again dried off. With the light rainfall of this region and exposure of the soil to sun and wind it seems doubtful if there is much penetration of moisture at any time. The soil may be perpetually somewhat dry due to its own intractability, and it certainly suffers from extreme lack of aeration.

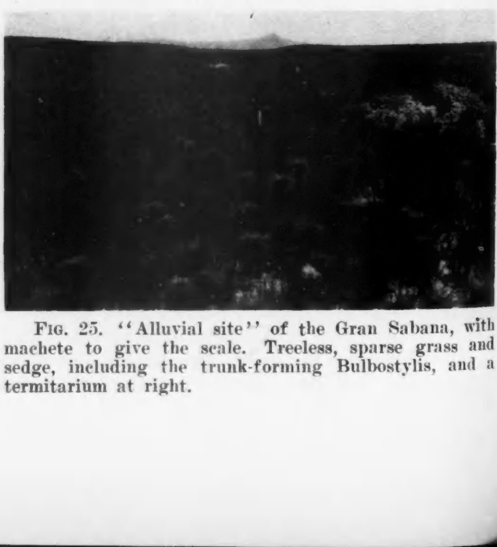

FIG. 25. "Alluvial site" of the Gran Sabana, with machete to give the scale. Treeless, sparse grass and sedge, including the trunk-forming Bulbostylis, and a termitarium at right.

The residual sites are those of upland flats, hills, knolls and scarps, with soil developed in situ or from ancient alluvia. A feature of these sites is the surface layer of stones and rocks, often so thick as seriously to impede the growth of vegetation (Fig. 26). The usual grass cover is formed by *Paspalum contractum.* The stones are generally sub-angular to rounded and of all sizes from ½ to 4 in. across, sometimes much larger up to the dimensions of irregular rocks several feet in length. Angular fragments of sandstone and rounded white quartz pebbles are seen but predominantly the litter consists of ironstone in lumps and nodules. There are never any termite mounds here and the vegetation is much reduced in stature and quantity. Small hairy sedges are often dominant. The soil below the surface stony litter is, curiously, entirely without stones and down to a depth of at least 5 ft. is a pink and white mottled clay loam, non-cracking, hard and compact, merging below into a pinkish-white clay-loam. There is no humus coloration at all in this soil and there are generally signs of active surface wash in progress in between the surface stones. The soils of steep slopes are similar except that rotten rock is often seen at shallow depth and the surface stone layer is reduced or missing.

FIG. 26. "Residual site" of the Gran Sabana, a knoll capped with stones and boulders, between which a few grasses sprout with difficulty.

Morichal soil has been described previously. Forest soils on the hills are seen to be a stiff, non-cracking yellowish-brown clay at the surface merging into a pink and white mottled clay at depth. They only differ from savanna soils of sloping ground in their surface humic coloration. Crumb structure is poor and they probably suffer from lack of aeration. The abundance of the palm Jessenia and the reduced, "dry evergreen" physiognomy of the forest are probably significant of this. These forests are in many ways reminiscent of the marsh forest at the Long Stretch in Trinidad (Beard 1944, 1946) where the soil is closely similar to that observed on the Gran Sabana. The topography of the two areas is unlike, however, the Long Stretch being flat. The forest soils of the Gran Sabana probably owe most of their superiority over savanna soils to the improved drainage conferred by slope. The possibility that many of the forest patches occur over intrusions of igneous rocks which develop a more favorable soil could not be investigated.

In "Exploración de la Gran Sabana" (Aguerrevere y otros 1939, pp. 596-631) Christoffel described a number of soil types from parts of the Gran Sabana not visited by the present writer. Some of these differ from those seen by the writer, others are similar. In a part of the valley of Kamarata the soil is derived from the disintegration of the nearby sandstone Auyán-tepui massif, and consists of three to five feet of grey or brown sand over gravel or boulder beds. The surface sand is loose and windblown. There are also stone-capped hill tops and some red clay soils derived from igneous rocks. The sandy soils are said to be well-drained.

The Luepa region of the north of the Gran Sabana has some very interesting soils. Christoffel's illustration of their profiles is reproduced in Figure 27. Profile No. 1 shows a sand-over-clay soil with iron pan. The uppermost horizon is a black sand a foot thick, over a ferruginous pan up to two inches thick, below which is a great depth of pale-colored, Kaolinitic clay. This is evidently a soil where drainage is impeded to an acute degree and it shows a typical formation of iron concretionary matter at the top of the impermeable horizon. This is the only soil-type reported from the Gran Sabana where there is actually an iron pan *in situ.* In places the pan is said to be greatly thickened and to crop out on the surface of the ground. This evidently gives a clue to the origin of the great masses of ironstone pebbles found littering the hilltops all over the Sabana. In

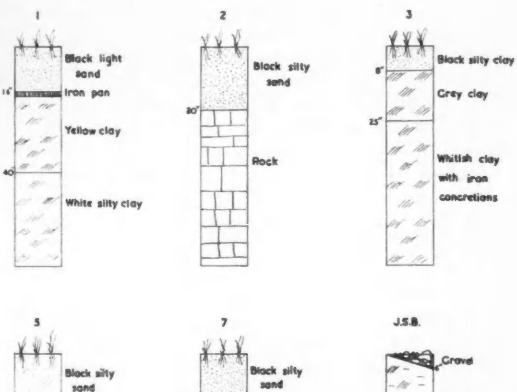

FIG. 27. Soil profiles of the Gran Sabana. Nos. 1 to 7 redrawn from Christoffel's profiles 1 to 7 of the Luepa district (in Aguerrevere and others 1939); "J.S.B. is a diagram of the soil as observed by the writer on the way to Roraima.

some past era sand-over-ironpan soils have presumably been more widespread and have disappeared by erosion leaving the remnants of the iron-pan on the surface of the clay horizon.

Profile No. 2 shows a predominantly silty, humic layer over a hard rock horizon. It is a savanna soil with drainage impeded as in No. 1.

Profile No. 3 while shown with grass tufts at the top, is actually taken in an aboriginal cultivation cut out of the forest. It is really a forest soil, and is a clay deeply colored towards the surface by humus.

Profiles 5 and 7 show a black, silty topsoil merging below a depth of two ft. into a pink and white silty clay which is stated to be impermeable. This is evidently closely similar to the "soil of alluvial sites" described by the writer, though the surface horizon may be of less compact character. Christoffel considered it suited to cultivation, whereas the soils seen by the writer certainly would not be. Even so, the soil is infertile and would need heavy manuring. The sandy soils of this region are clearly infertile, consisting largely of pure quartz, and would not lend themselves to crop-production. In the case of these loamy soils Christoffel seems to have been over-impressed by their favorable texture, and suggested cultivation of wheat and many other field crops as well as fruit trees and Cinchona. The adverse drainage factor appears not to have been considered. Attempts to cultivate the savannas in Trinidad have failed very miserably. On the Rupununi savannas of British Guiana crops are only cultivated in old cattle corrals. The aborigines studiously avoid cultivating savannas and invariably make their gardens in the forest. Christoffel's viewpoint, stated in a long preamble, is that the whole region was formerly covered with forest which has been destroyed and converted into savanna over a very long period of years by the encroachments of the Indians who fell patches of forest for cultivation and subsequently burn off the secondary vegetation repeatedly, so that grass takes possession. During this process the soil is progressively impoverished and loses its humus, and is then incapable of going back to forest "A clear proof of the infertility of these lands is the poor vegetation which covers them" (p. 600). To one taking this view it is clearly only a question of suitable treatment, working of the soil and improvement with green manures, to bring it back into good condition.

Conditions around Santa Elena and to the southward are somewhat different from the Gran Sabana proper since the Kaieteurean sandstones have given way to rocks of the basement complex. North of an east-west line through the village is a series of scarps formed by northward dipping quartzites, whose vegetation has already been described. Immediately south of the village in an east-west direction runs a range of high, rounded hills due to a basic igneous intrusion and south of this across into Brazil is a region of undulating country upon mixed igneous and metamorphic rocks. All of this area, both the hills and the undulating country, is about equally covered with forest and savanna in a highly haphazard manner and there is no apparent correlation between vegetation and topographic factors. Savanna sometimes ascends to the tops of the highest hills, but just as often these are forested. Some of the forest land in the neighborhood of Santa Elena has been cleared for agricultural purposes and is said to be fertile. The plantations appear to be doing well and are yielding good crops of sugar cane, plantains, maize, cassava and other root vegetables. A soil profile examined at the hacienda of Coronel Mendez showed a stoneless clay soil, brown, crumbly and cracking at the surface with plentiful humus and small roots, merging gradually to a dark red clay below 3 ft. depth. The distance to which the igneous rock had decayed could not be ascertained. This appeared to be a normal "red earth" soil developed over basic igneous rocks. The forest occurring on this soil is a luxuriant evergreen seasonal forest. Most of the component species were unknown to the writer but it corresponds in physiognomy closely to the evergreen seasonal forest in Trinidad. It is much taller than the forests seen out on the Gran Sabana, with stouter trees, a greater variety of strata, forms and species, and several deciduous species are present. Towards the hilltops there is some reduction and assimilation to the dry evergreen type, with abundance of Manilkara trees. This is presumably due to the shallowing soil and exposure to wind. The occurrence of evergreen seasonal forest here where the rainfall is not likely to differ substantially from other parts of the Gran Sabana tends to show that the forests on the Kaieteurean sandstones are a special type due to adverse soil conditions.

The boundaries of forest and savanna in this area are abrupt, large trees rising straight from the edge of the grass. Areas of dead and burned forest were not seen by the writer. There is likewise an abrupt change in the soil on entering the savanna. It becomes bright red instead of brown at the surface and is thickly sown superficially with pebbles, stones and rocks apparently of an ironstone conglomerate. There was no opportunity to examine the subsoil but it may be that undecomposed rock lies close to the surface. The difference between forest and savanna soils would then be similar to that observed near Upata in Venezuelan Guiana. The geology of the basement complex on the Gran Sabana is imperfectly known and it may be that different geological formations underlie the savanna and forest areas, the one weathering readily into a deep forest soil and the other being resistant and forming a perpetually shallow site. The only other possible explanation would be that forest formerly covered the whole area but was destroyed by fire in certain parts which then became severely eroded and were reduced to rocky, shallow sites. If the forest soil profile which the writer investigated is a typical one, this explanation would not account for the superficial mass of ironstone in the savannas. Further it is much easier to imagine a whole stretch of country being burned off than small patches which are not readily set fire to

repeatedly. In crossing this country the writer crossed a small patch of savanna which had evidently not been burnt for years. The grass was breast-high in parts and densely, almost impenetrably tangled, including a certain amount of unpleasant cutting sedge (Scleria). The ecological relationships of forest and savanna here are obscure at present and require further detailed study.

THE RUPUNUNI—RIO BRANCO SAVANNAS

Two detailed studies exist of the savanna region of interior British Guiana and the adjoining portion of Brazil, by Follett-Smith & Frampton (1935) and Myers (1936). Myers stated that this region was bounded on the north by the Pakaraima mountains of British Guiana (to the east of Roraima and forming the Amazon-Essequibo watershed), on the west by the "Parima mountains" (apparently the "Sierra de Pakaraima" of the Venezuelans on the Gran Sabana), and on the south by the great equatorial forest of the Amazon with the River Mocaja-i, a tributary of the Rio Branco, forming the exact boundary. To the east and south-east the boundaries are not well known and presumably the savanna country of the Surinam-Brazilian border is contiguous. The Gran Sabana is actually contiguous with this region also, the Sierra de Pakaraima (or Parima) beeing only patchily forested where it divides the two. In British Guiana the savannas are divided into two by the Kanuku mountains. A map of the region is given by Myers.

This region does not consist of a definite plateau like the Gran Sabana, the elevation varying from only 200 ft. at the junction of the Rios Branco and Mocaja-i to 4,500 ft. at the Orinoco-Amazon watershed. Most of the country is mountainous or undulating but still preserves, particularly on the highest lands, a tabular structure.

No climatic data were given by Follett-Smith & Frampton but Myers stated that "the lower savannah climate is essentially similar to that of the llanos—a restricted season of heavy rains and a long dry season, leading to the same effects on the vegetation. In the wet season large tracts are under water; in the summer the land is parched for long distances, and even drinking water is hard to procure. The savannah vegetation is thus of climatic origin" (p. 166). Myers qualified this, however, on p. 176 by stating that "we are justified in regarding the present vegetation as a fire climax."

This region is not so consistently grass-covered as the Gran Sabana. Myers noted the constant alternation of savanna and forest, plain and mountains. "Occasionally, on the Uraricuera savannahs, one sees vast level plains, very reminiscent of the llanos, without so much as a bush or a hillock to the horizon. Usually, however, on the most open, level and treeless stretches of savannah, there is always forest in sight, either in the form of fringing woods along one of the numerous rivers, or as bush islands, large or small, while mountains, either the Kanukus, the Pakaraimas or some of the isolated savannah ranges, usually close at least one horizon."

The soil analyses given by Follett-Smith & Frampton, show in all cases that, throughout the region they examined, forest soils are only slightly more fertile than savanna soils. There is little essential difference in chemical composition between them. There are, however, considerable differences in drainage since their savanna soils are mainly on flats subject to inundation in the rainy season and their forest soils mainly on mountain slopes. Their description of the main soil types agrees exactly with those seen by the writer on the Gran Sabana, viz.: "The elevated soils usually fall into two main classes (a) a highly acidic grey or buff sandy topsoil which merges into a highly acidic clay loam subsoil of pinkish color and (b) a highly acidic red clay topsoil often covered with a layer of ironstone gravel and resting on a highly acidic red clay subsoil. The soils of the swampy flats consist of pale colored sands, silts or clays often covered by a thin layer of acid organic matter." In general the Rupununi savanna soils seem to be more often sandy at the surface than those in the part of the Gran Sabana seen by the writer, though other parts of the Gran Sabana appear comparable.

Trachypogon plumosus is the dominant grass throughout the region and on Myers' estimate it forms 90% of the total population. Important subsidiary grasses are *Aristida setifolia, Axonopus aureus, Andropogon angustatus* and *Mesosetum liliiforme*. Woody elements include the recumbent *Byrsonima verbascifolia,* and the shrubs *Curatella americana, Byrsonima crassifolia, B. coccolobaefolia, Bowdichia virgilioides, Plumeria* sp., *Roupala* sp., *Psidium* spp., and *Anacardium occidentale*. Myers found these to be usually more scattered than in "orchard" formation, but they are evidently more common than on the Gran Sabana. Riverain flats, particularly at the higher elevations, are covered with *Sporobolus cubensis*.

A feature of the Rupununi-Rio Branco area is the *baixa* or swampy depression, covered with sedges and inundated for half the year. Many of these *baixas* are several miles across, with groves of Mauritia palms occupying the position of "bush islands" in them. They are evidently analogous to the *esteros* of the Orinoco llanos. According to Myers, "the determining factor between sedge flat and *Trachypogon* savannah is apparently the duration of flooding. The latter type can endure flooding for a limited time, while the former cannot stand desiccation." Areas of this nature were not seen on the Gran Sabana.

Some additional facts of significance can be obtained from Schomburgk's account of his travels (1847). This author repeatedly mentioned the stony surface of the savannas, encountered everywhere except on the swampy depressions. The ground was strewn with quartz and granite fragments or pebbles and boulders of ironstone conglomerate. In travelling

up the rivers he observed that wherever savanna came right down to the river's edge, thus permitting a section of the savanna subsoil to be seen in the river bank, it generally consisted of a ferruginous conglomerate covered only with a shallow soil, whereas the gallery forests were underlain by deep alluvial soil. Termite mounds were mentioned as a feature of rising ground in the savannas. These might be as much as 12 ft. high and were of irregular shape—"now they formed spiral pyramids, now columns with capitals, or resembled giant mushrooms with brimmed tops." These ant-heaps were said to be devoid of all vegetation. A second species was found to form low flat mounds on the lower parts of the savanna and this is presumably the same species as found on the Gran Sabana.

The Amazon Basin

The Amazon is the largest river system in South America, draining 40% of the surface of the continent. For the most part the basin is extremely lowlying. Ocean-going vessels ascend the stream as far as Iquitos which is 2,500 mi. from the ocean and less than 500 ft. above sea level. It is therefore readily understandable that enormous areas are subject to inundation in the rainy season and alluvial sediments are being deposited there. The lower course of the river flows between the Guiana and Brazilian highland masses, in which the lower tributaries originate. The upper tributaries rise in the Andes and drain a large basin floored with Mio-Pliocene sediments. Although the river now flows east to the Atlantic, until mid-Miocene times it flowed west to the Pacific. Elevation of the Andes then obstructed the drainage and caused the formation of enormous lakes in which the sediments referred to above were deposited. Eventually a new outlet was cut to the Atlantic, the lakes drained, and more recently a new cycle of sedimentation has begun along the lower course.

Active sedimentation along the courses of the rivers has caused them to become embanked by strips of relatively raised ground known as "restingas." Behind these natural bunds lie enormous depressed areas, particularly along the lower Amazon, which are either perpetually filled with stagnant water or are subject to seasonal flooding by the rise of the rivers during the rainy season. Land of the former type is known locally as "igapó" and of the latter type as "varzea." Some distance back from the watercourses is the higher ground out of reach of the floods, known as "terra firme."

The upper Amazon, defined as that portion of the river and its tributaries lying above the confluence with the Rio Negro, is distinguished by different natural conditions from the lower Amazon—the portion of the stream below the Rio Negro down to the head of the delta—and both these two regions differ again from the delta itself.

The delta is entirely a lowlying region, much of it permanently below water level, a maze of creeks and distributaries bordered either by restingas with permanently swampy igapós behind them or by varzea land which is flooded diurnally by the ebb and flow of the tides. In the centre of the larger islands there is older alluvial ground high enough to be considered terra firme. The delta has a high rainfall; for example (Bouillenne 1930), there was recorded at Para in the delta an average rainfall from 1894 to 1911 of 2486 mm annually (103 in.) distributed in 252 rainy days. There is a very wet season from January to August, followed by a pseudo-dry season, also rainy but receiving the precipitation in heavy showers instead of unrelenting downpours.

The lower Amazon region above the delta, on the other hand, has a relatively much drier, more seasonal climate. Again according to Bouillenne, Obidos in this region receives only 1592 mm of rain annually distributed in 157 days, most of which are confined to the rainy season. The alternate season is now no longer "pseudo-" but actually a dry one and its influence is reflected in the character of the vegetation on terra firme. The river courses here are mainly bordered by restingas enclosing here and there swampy igapós but more generally varzeas which become deeply covered by water poured off from the main river during flood, and completely dry during the low season. Tides are no longer felt here. Owing to the flooding of major tributaries of the Amazon at different seasons, the duration of the flood along the lower course is about 8 months. The lowest varzeas are covered for the whole of this period, the highest for some weeks only. The water level rises during flood from 6 to 9 m annually (Bouillenne 1930). Terra firme comes in many places very close to the main stream and, since this is the area through which the Amazon carved its new course to the eastward in Plio-Pleistocene time, consists of low hills and plateaus formed of ancient continental rocks. Between Prainha and Obidos, on the north bank, Bouillenne described an intermittant escarpment edging a plateau of these rocks rising some 300-400 m and set back 25 to 50 km from the river. These low hills form the connecting link between the highland masses of Guiana and south-central Brazil.

The upper Amazon is again a rainy region, receiving from 80 to 100 in. annually, the dry seasons being short and only moderately severe. There are two rainy and two dry seasons in the year, most of the rain falling between October and June. In the north of this region, granites of the continental basement come to the surface but the major portion of the geology consists of the Mio-Pliocene lacustrine sediments, forming a vast plain across which the rivers meander. As lower down, there are seasonally inundated lands, the rise of the rivers being even greater, though for a shorter period. For the most part, the land appears to be terra firme.

The whole Amazon basin is covered for the most part with forests, which have become almost legendary as the archetype of equatorial rain forest. This great jungle, dense, gloomy and impenetrable, is supposed to extend in unbroken, impressive vastness for thousands of miles. Whether such a popular

impression is justified is another matter. In the words of Bouillenne (1930), "the exuberance of the forests and the humid nature of this equatorial region are well known and commonly pass as geographical dogma. None the less, the virgin forest is broken all of a sudden by patches of the poor vegetation of numerous savannas. . . . The presence of savannas in Amazonia is a surprising fact." And it is not only the radically divergent formation of the savannas which must be separated from the equatorial rain forest. The actual forests of Amazonia are very diverse both in form and in habitat. As the writer has previously remarked (1944), it is doubtful if the bulk of the forest in Amazonia can truly be considered as rain forest except in the widest sense of the term.

It will be desirable to consider separately the vegetation of the three regions of the Amazon.

THE AMAZON DELTA

Since the bulk of this region lies below flood level, we shall naturally find that the vegetation is predominantly of swamp type. On the terra firme of alluvia which now lie above flood level there are both rain forests and savannas. A whole belt of savannas, in fact, runs along the Atlantic littoral from the border of French Guiana to the island of Marajo in the Amazon mouth. This belt is a continuation of the savannas of lowland Guiana and as Benoist has remarked for French Guiana it characterizes a zone of Pleistocene alluvia between the coastal swamps and the interior forests. According to Ducke (1938), these savannas are characterized by the presence of the tree *Hancornia speciosa*, which may be taken to indicate that the flora generally resembles that of the savannas on the South Brazilian plateau.

THE LOWER AMAZON

The restingas which border the rivers in the lower Amazon are forest covered. This is described as varzea forest, though generally inundated for only short periods. Similar varzea forest occurs on the landward margin of the flood plain, but in between there are large open expanses known as *campos de varzea*, which we may translate as "seasonally inundated savannas." Behind a thin screen of trees on the restingas lie these large open stretches, covered deeply with water in the flood season, grassy in times of low water. Describing the scene from a commanding hill top at Monte Alegre, Bouillenne (1930) wrote: "This expanse of watery, herbaceous flats is astonishing. Where are the deep forests of the Amazon? One scarcely notices the thin strip of marginal forests. Travellers who have not left the banks imagine immense forests. But behind these, there are only varzeas."

There is forest growth on the varzea here only where the inundation is not too deep. In the swamp forests of the igapós the water, though permanent, is not deep and in the palmaceous marsh forests of the delta the flood water ebbs twice daily. In these *campos de varzea* water stands for months to a depth sometimes of over thirty feet, and we find in consequence a specialized grassy vegetation. Three species of grass were mentioned by Bouillenne: *Panicum amplexicaule*, *P. spectabile* and *Paspalum repens*. At low water, when the ground is exposed, these grasses have the aspect of an ordinary tall grassland. As the flood begins and the water rises, the grasses rise with it and form floating mats. Frequently these mats become detached by the current and float away down stream, the grasses still living and vegetating.

Perpetually swampy places in the *campo de varzea* which never dry up are filled with Montrichardia. Trees of *Salix martiana* line creeks and thickets of *Alchornea castaneifolia* occur on the transition to varzea forest. There are no other trees. It is clear that in these campos, as in the wet savannas of British Guiana, we have correctly herbaceous swamps and not savannas at all. The physiognomy of hygrophilous grasses forming a floating mat upon deep water constitutes one of the sub-types of Herbaceous Swamp in the Beard classification.

The forests of terra firme on the lower Amazon appear to be evergreen and semi-evergreen seasonal forests, for the most part, judging from the accounts of observers. They are broken in many places by campos which in this case are true savannas, raised well above flood level. One of our best accounts of these is due to Bouillenne (1930) who visited certain savannas both on the south bank at Santarem and on the north bank at Monte Alegre. These savannas are surrounded by forest with the usual abrupt boundaries and occur over ancient continental rocks on sites which are predominantly flat or at most gently sloping. The savannas at Santarem slope gently up from the river Tapajoz rising at the back into low hills (Spruce 1908). At Monte Alegre they occupy more or less flat plateau sites or the gentle dip slopes of scarped ranges of hills (Bouillenne). The soil is a loose sand on the flat portions and a clay strewn with stones on the hilly portions. Spruce remarked that at Santarem "the soil is mostly a loose white sand, but the hills are strewed with volcanic scoriae and towards the summits appear volcanic blocks of considerable size." It was a source of wonderment to Spruce that he should find this material which he took for volcanic lava "at various points in the Amazon valley," without a sign of any volcanoes. He described it as "a honeycombed rock with a reddish vitrified surface, quite resembling masses of slag." In the light of modern knowledge it is quite clear that this material is actually concretionary ironstone, such as we very frequently find associated with savannas. Bouillenne, a more recent observer, described the stone littering the savanna at the Serra de Itauajury as a brownish, angular sandstone veined with "filons limoniteux." The soil beneath the adjoining forest in these parts is said to be tropical red earth and this presumably underlies the sandy or stony top layers of the savanna, though we are not told so. The forest occupies the more broken country such as the steep scarp-

faces of the hills and the valleys and ravines. It occurs also as gallery forests in the savannas.

According the Bouillenne there are three types of savanna to be distinguished. The flora is much the same throughout and the types are differentiated mainly by the form or disposition of tree growth. The most general type of savanna is the common "Orchard" form, known as *campo cerrado* in Brazil —the *chaparral* of Venezuela. Small gnarled trees of no great height and numerous shrubs are scattered here and there over a herbaceous stratum of the usual type of bunch grass and sedges and flowering herbs. In very stony places and the higher ground the trees thin out becoming rare and stunted, so that the savanna could almost be classed as open. Thirdly, there is what Bouillenne called Parkland, with the savanna trees up to 10 m in height, closed up into clumps of bush with shrubs collected at the foot of the trees. This appears to be an unusual aspect of the savanna and Bouillenne remarked that he had not encountered it elsewhere. "Bush islands" are a feature of the Guiana savannas, particularly in the moister parts, but they are formed of forest, not savanna, trees. The closing up of the savanna trees to a regular stand suggests the *catanduva* of south Brazil.

The trees are short, gnarled, brittle, and thick barked. Their leaves are few, large, vertically hanging, stiff and brittle, generally simple, waxy or felty. Few have scaly buds, a usual feature of xeromorphic plants, and few are thorny. Bouillenne claimed that most of the trees and shrubs are deciduous, contradicting other observers who have held that they are evergreen.

Herbs and subshrubs are tufted, with bare soil between plants, and grow to a height of 1 to 2 ft. Subshrubs are mainly formed of multiple shoots sent up each year from a woody rootstock. Herbs have underground perennating organs, which do not act as water storage tissue to any extent. Annual herbs are rare.

Bouillenne made no mention of the names of grasses, except at Santarem. Here Spruce noted "but one species of Paspalum in scattered tufts." Bouillenne named *Andropogon virginicus, Sporobolus indicus* and a sedge, *Rhynchospora* sp. The trees belong to numerous species, among which may be mentioned *Anacardium occidentale* and *A. microcarpum, Curatella americana, Bowdichia virgilioides, Aeschynomene paniculata, Salvertia convallariodora, Qualea grandiflora, Vochysia ferruginea, Byrsonima poeppighiana* and *B. coccolobifolia, Xylopia grandiflora, Sclerolobium paniculatum.* Melastomaceae are prominent among the shrubs, among which may also be mentioned *Byrsonima verbascifolia, Tecoma caraiba, Polygala spectabilis, Rhabdodendron amazonicum,* species of *Cassia, Calliandra, Crotalaria, Eugenia, Mouriri.* At Monte Alegre *Qualea grandiflora* is mentioned as extremely abundant and the commonest of the trees.

Spruce described a slightly different type of savanna near Manaos in a wetter region. The soil was said to be a stiff clay, the vegetation grasses and sedges in tufts with a Scleria conspicuous, Utricularia, Drosera, 3 orchids, a Polygala, several rubiads, the shrubs including several melastomes, Byrsonima and Curatella.

The flora of all these savannas is essentially that of the Brazilian plateau, though much poorer in species. The Amazonian savannas must be regarded as off-liers of those on the higher ground to the southward. In spite of their stronger floristic affinity with the south, the Amazonian savannas form a connecting link between the wide savanna regions of the Guiana and south Brazalian Highlands. There is no continuous connection, at any rate at the present time, but savanna patches of varying size from small to large are scattered at no great distance from one another from the edge of the Amazon floodplain in both directions towards the highlands. North of the Amazon, towards the frontiers of the several Guianas, according to Ducke (1938) the country is covered, outside the riverain forests, with expanses of low, dry forest of the type called *campina-rana,* and *campos.* These savannas are in connection with those of the Rupununi-Rio Branco on the highlands and with those of the Brazil-Surinam frontier region noted by Pulle (1938). They extend, according to Ducke, from the upper Rio Branco by way of the headwaters of the Trombetas to the upper Jari. They are said to be in part high-lying and dry, in part low and swampy. They share the *flora geral* of the South Brazilian savannas though on the Rio Branco there are found some species which have come down from Venezuela.

In a southerly direction we have less positive information. It seems that there are fairly frequent occurrences of savannas on the higher ground between the rivers, but we know little about them since the rivers themselves are bordered by forests and few travellers wander far from the streams.

Bouillenne was of the opinion that the causes for the presence of savannas on the lower Amazon are climatic. The lower Amazon has a more seasonal climate than the upper Amazon and this would be the major cause of the savannas, though not the only one, for the climate as it stands is quite able to support forest. In Bouillenne's view, the savannas are all to be found located in the lee of some topographic obstacle and thus occupy small rain-shadows, patches of "less atmospheric precipitation." Fires, he considered, have had no important effect other than to keep sharp and abrupt the boundaries of the savannas. Cattle are too few and too recent in their arrival and the effect of man is also held to be insignificant. While admitting that in general savannas are on sandy and stony soil and forest on clay, Bouillenne could not admit that the soil had anything to do with the question, because, in his view, first the bulk of the Amazonian forests are on sand, and secondly, the same sandy and stony soil carries both forest and savanna, witness the gallery forests.

THE UPPER AMAZON

The Upper Amazon basin, a relatively little known region, appears to be devoid of savannas. Ducke (1938) described it as an immense plain covered with luxuriant forest, not all of which is very tall. Even here, the rain forest is not universal, being broken by substantial areas of lower growth, *campina* and *campina-rana* ("Bastard campina"), particularly in the region of the Rio Negro.

The *campina-rana* is also known as *caa-tinga* though it is not the same as the caa-tinga of the Brazilian north-west which is thorn and cactus scrub. The name caa-tinga was said by Spruce (1908) to mean "light forest" in Lingoa Geral, referring to the lack of shade cast by the open canopy. These types are associated with deposits of white sand derived from granite and are therefore to be found where the ancient rocks come to the surface rather than on the Tertiary sediments.

DISCUSSION

NOMENCLATURE AND CLASSIFICATION

The writer proposes to confirm the use of the name "savanna" for the plant formation to which the natural grasslands of tropical America belong, because as Lanjouw showed (1936) this is historically correct, the aboriginal word from which "savanna" is derived being a local name for that formation. Whether there is sufficient affinity between the grasslands of tropical America, Africa, Asia and Australia to permit the wider use of the name for a world "formation-type" the writer is not prepared to say, having no personal knowledge beyond the Americas. If we establish the name "savanna" as the correct one on historical grounds for neotropical grasslands, however, it will be legitimate for others to apply it to those of the old world if they consider there is sufficient affinity in physiognomy and ecological relationships.

In an earlier paper (1944) the present writer advocated that the plant formation should be regarded as a physiognomic unit into which are grouped numerous floristic associations showing equivalent structure and life-forms. In keeping with this view, savanna will be discussed here as a physiognomic entity. The information collected in the earlier part of this study is sufficient for a grouping and classification of savanna types on such a basis and it will be possible to delimit certain subordinate physiognomic units or sub-formations. The available information is not yet detailed enough over sufficiently wide regions to enable floristic associations to be recognized and in this respect it will only be possible to indicate the composition of certain known communities belonging to the sub-formations.

All American savanna is sufficiently homogeneous to be regarded as a single formation, corresponding to that originally defined in the writer's paper of 1944. The more detailed study carried out here does not appear to necessitate any departure from the earlier viewpoint. It may perhaps, however, be desirable to attempt a more precise definition of the formation. In 1936 Lanjouw proposed this definition in supersession of earlier ones:

"Savannahs are plains in the West Indian Islands and Northern South America covered with more or less xeromorph herbs and small shrubs and with few trees or larger shrubs."

While this definition marked an advance on its predecessors, it is now open to several objections in detail. If we are to regard it as a physiognomic unit the savanna should not be defined by any environmental factor, and the word "plains" should be omitted. The essential unity of savannas throughout tropical America revealed in this general study makes undesirable Lanjouw's restriction as to locality, made on historical grounds. If the type of a botanical species were collected say in Mexico, we cannot for that reason exclude from the species plants collected outside that country.

Finally, Lanjouw's definition of the woody element implies that trees and shrubs must always be present, which is not the case. Bews (1929) very rightly pointed out that it is "unnecessary to separate tree savanna from pure grassland since the presence of trees does not alter the composition of the latter, and any differences in the grass flora that may exist between pure grassland and tree savanna depend on climatic and soil differences. As a matter of fact, the differences between the grasses of tree savanna and pure grassland savanna are, floristically, very slight." This observation was based upon African conditions but is equally applicable to American.

Robyns (1936) proposed this definition in preference to Lanjouw's:

"Savannas are open herbaceous communities, mainly of grasses, with or without a scattering of tropophilous trees and shrubs, localized in the tropical regions with a well marked dry season during which they dry up generally, and differing from steppes as much from the ecological point of view as from the floristic."

This is in some ways a better definition. However, if savanna is to be a physiognomic unit we must not admit habitat factors to the definition, and the localization of savannas in regions of well-marked dry season is not correct.

The writer proposes the following definition:

Savannas are communities in tropical America comprising a virtually continuous, ecologically dominant stratum of more or less xeromorphic herbaceous plants, of which grasses and sedges are the principal components, and with scattered shrubs, trees or palms sometimes present."

The essential point is that the herb stratum is ecologically dominant. This definition appears adequately to separate savanna from all forest and woodland types, from the Andine *paramo* and *puna*, and from herbaceous swamp.

Warming (1909) allocated tropical grasslands to True Savanna and temperate to Grass-Steppe, including in the latter the steppes of Russia, the prairies of North America and the pampas of Argentina.

This is a very acceptable view, and the present writer urges that the names steppe and prairie should be restricted to temperate grasslands, whose ecological relationships are quite different from the tropical. Warming set up two other categories, Thorny Savanna Vegetation and Savanna Forest. The former includes open thorny bush types with grass and in the Americas refers both to artificial grasslands of some grazing areas which are not correctly savannas and to vegetation like that of the Chaco which is really a mosaic of savanna and thorn woodland as separate formations. Savanna-forest may perhaps describe *catanduvas* or *cerradões* of Brazil and warrant consideration as a separate but related formation.

In classifying subordinate groups within the principal savanna formation, reference should be made to the work of Bews (1929) which, although based on African experience, is essentially so sound that it is directly applicable to the Americas. Bews made the following classification of tropical grassland types, based upon the morphology and evolution of the grasses, and there is no reason why we should not endeavor to apply it to our American conditions:

1. Forest margin and hygrophilous types.
2. High-grass savannas.
3. Bunch-grass savannas.
   (a) Tall bunch-grass savannas.
   (b) Short bunch-grass savannas.
4. Tropical alpine grasslands.
5. Semi-desert and desert types.

In the present study we are concerned with groups (2) and (3), which it should be possible to recognize in tropical America and to constitute as subformations of our savanna. Two major factors seem, however, to lead to important differences in American conditions—the relatively weak assault, hitherto, by man and animals upon the vegetation, and the generally higher rainfall. These interact, for under moister conditions, fire is not so frequent nor so intense and the plant cover recuperates more quickly. On the African continent areas with more than 40 in. of rain a year on the average are an exception; in South and Central America they are the rule. The only parts of tropical America where the average annual precipitation does fall below 40 in. are the Pacific coastal desert in Peru and Chile, the Andean *puna*, the Brazilian North-west, the Guajira and Paraguaná peninsulas of the Caribbean and the Paraguayan-Bolivian Chaco. For these reasons, as will be seen, it may not be possible to recognize High-Grass Savanna in the Americas. Tall Bunch-Grass Savanna is the predominant type. Short Bunch-Grass Savanna is doubtfully recognizable (being associated with rainfalls under 35 in.) and it will be desirable to define an additional subformation, Sedge Savanna, found in certain areas of very high rainfall. The Tall Bunch-Grass Savanna is capable of further subdivision into four phases (Open, Orchard, Palm and Pine) according to the type of woody growth present (or absent).

Physiognomy and Composition

We may now examine and define in detail the various types of savanna which it is possible to recognize, these being:

1. Tall Bunch-Grass Savanna: the predominant type—in fact the neotropical savanna *par excellence.*
2. Sedge Savanna: associated with high rainfalls.
3. Short Bunch-Grass Savanna: low rainfalls.
4. High-Grass Savanna: a doubtful type.

Tall Bunch-Grass Savanna

To typify the tall bunch-grass savanna we cannot do better than to take up Warming's original exposition from Lagoa Santa (1892), although strictly this lies outside the area of the present work. This was the first good and thorough description of the formation in modern ecology and may therefore claim priority as a definition. If we wish to borrow from botanical practice, we may regard this of Warming's as the first publication of the description of the type, and the type locality as being Lagoa Santa in Brazil. To qualify for classification as tall

FIG. 28. Original sketch by Eugen Warming of the neotropical savanna at Lagoa Santa, Brazil (1892).

bunch-grass savannas, other communities must correspond sufficiently closely to this type. The following is a translation from Warming's original Danish in "Lagoa Santa," p. 244:

"Lagoa Santa's campos are thus a plant formation which mainly and in all its modifications is characterized first and foremost by perennial grasses growing in slender tufts at intervals and other herbs, particularly composites, together with subshrubs whose height for the most part is ⅓-⅔ m (1-2 ft.), and over whose flower-decked expanse may rise bushes and low, crooked and gnarled trees with open crowns and in a more or less close stand (campos cerrados), but never under natural conditions in such a close stand that one cannot pass through it unhindered in all directions. The entire Flora has a xerophilous, but not strongly xerophilous character which expresses itself in the coarse, often hairy, greyish leaves of the grasses and of many other plants, in the stiff, leathery or densely pubescent leaves of the trees and bushes and of certain herbs, in the trees' gnarled form, in the frequency of essential oils and so on. Next must be emphasized the frequent appearance among both herbs and shrubs of underground, irregular but often tuberous growths and among trees of great thickness of bark, as well as the lack of lianes

and epiphytes and especially also of epiphytic mosses and lichens as well as these latter growing on the ground. Finally may be added what I shall a little later have to say in the section on the seasons, that all trees and bushes are deciduous, so that the leaves can usually live about 12 months and in many cases fall off before they have attained this age. The vegetative period may, on the whole, be said to extend over the whole year. But the campo vegetation is not a strongly xerophilous vegetation and has nothing of the most marked characteristics of the steppe or desert: thus, annual plants are very rare, bulbiferous plants and succulents are absent, thorny bushes extremely scarce and finally, there are not few plants whose organs of transpiration are reduced in that the leaves are narrow, small or divided, but this is not carried to such an extreme as in steppes and deserts.''

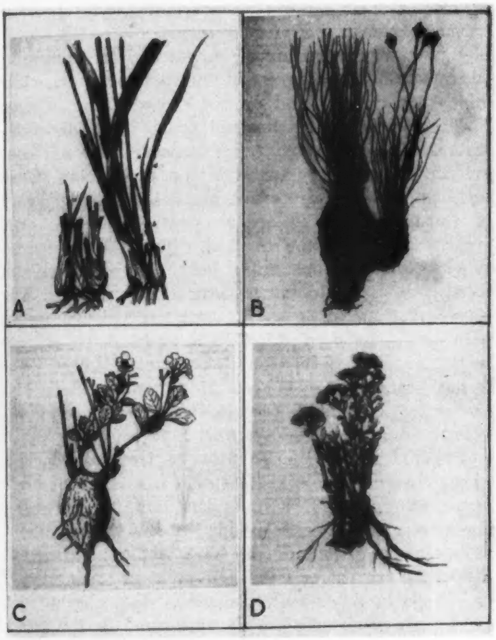

FIG. 29. Sketches by Eugen Warming (from *Lagoa Santa*, 1892) of the life forms of savanna plants.
A.—*Andropogon villosus*, a typical bunch-grass.
B.—*Bulbostylis* (*Scirpus*) *paradoxa*, the sedge with thickened aerial stem.
C.—*Casselia chamaedryfolia*, a forb with tuber.
D.—*Baccharis humilis*, a suffrutescent shrub with rootstock.

This type of savanna, according to Bews, is the most extensive in the world and certainly all the savanna in America belongs to it with the exception of the limited areas under sedge or short grass. Throughout tropical America these savannas exhibit a remarkably high degree of uniformity in flora and differ markedly in this respect from the forest formations.

The community is dominated by a moderately dense layer of herbs among which *Gramineae* generally number over 90% of the individuals. *Cyperaceae* are nearly always present and may cometimes (where conditions begin to approach those of sedge savanna) become almost co-dominant with the grasses. The remainder of this stratum is composed of dicotyledonous herbs and procumbent woody plants. The height of this herb layer is normally between 14 and 20 inches, but it will increase to about 36 in. if it remains unburnt for several years. During the flowering season, the spikes of the grasses reach 3 to 5 ft. in height. The growth of the herbs is characteristically tufted, in the form of a bunch of stems springing from an underground rhizome or rootstock, rather than of a plant with a basal rosette of leaves. It has been estimated (Martyn 1931), that these tufts occupy 60% of the soil surface (see Fig. 6). The rest is quite bare, though normally concealed by the spreading stems and leaves of the tuft-plants. Where there is a tendency to "hog-wallow structure" the soil between the tufts is excavated and upstanding tussocks are formed. During the dry period when growth dies down, the soil is visible and its color becomes apparent at a distance.

The grasses and sedges are of xeromorphic structure, coarse, tufted plants, their leaves invariably narrow and harsh, often rolled and hairy, many of them with sharp, cutting edges. Only fresh young growth is really palatable to grazing animals. The dicotyledonous herbs belong mostly to the Compositae and Leguminosae and are practically all perennial with an underground tuber or rootstock which is not usually water-storage tissue but a simple perennating organ enabling the plant to withstand repeated fires. Most of the herbaceous plants spring into activity early in the rainy season, put out new leaf growth, and flower. If the soil becomes waterlogged later in the rains, they die down into a dormant state which in any case supervenes on the arrival of the dry season and is continued until the following rains. Grass roots ramify thoroughly through the top soil and where a claypan is present they are capable of penetrating the subsoil deeply.

Scattered shrubs are generally present, so many of them being procumbent and having underground, perennating organs that is is frequently difficult to make an exact distinction between herb and shrub. There are three principal types of shrub. The first, typified by *Byrsonima verbascifolia* and *Palicourea rigida*, consists of an underground stem which protrudes above ground level sufficiently to give off a rosette of large, stiff leaves which lie upon the ground. The second type also has an underground woody stem or rootstock from which after every fire a bunch of herbaceous or woody shoots is sent up. These may reach a height of two to three feet and the whole plant may form a miniature thicket ten feet in diameter. The third type is a single-stemmed, low shrub 2-3 ft. high like a small tree. Succulents (*Cactaceae*, *Agave*) are very rare in savannas. There is an almost complete absence of epiphytes, lianes, mosses and ferns, but there are some woody plants of scandent habit which are found to be related to forest lianes.

The amount of tree growth present is very variable and the writer has proposed a division of the Tall Bunch-Grass Savanna into four phases according to the type of tree growth present, or its absence. *Open Savanna* is completely or virtually treeless, though shrubs of the *Byrsonima verbascifolia* type will frequently be present. Almost the whole of the Gran Sabana area of the Guiana highlands is of this type. Elsewhere it comes in as local patches usually on river flats or the flat tops of ridges. *Orchard Savanna* comprises a growth of small trees which invariably assume a characteristic, curiously gnarled, bent and twisted form. Both the height of these trees and their density are enormously variable. For the most part they are between 10 and 20 ft. in height and 20 to 30 ft. apart, but there may be almost treeless areas with an occasional specimen 4 ft. in height or dense stands 40 ft. high forming almost a forest. The form of these trees is a very characteristic feature and may be appreciated from the photographs reproduced with this monograph. There is seldom any definite trunk, numerous branches arising low down, and these are bent, twisted, crooked, leaning or otherwise distorted. A more or less domed crown is produced. The branch wood is very brittle. Bark is thick, corky, corrugated, generally sloughing off in large flakes: it is fire-resistant.

The thorny, microphyllous type of tree, such as is typified by the genus Acacia, is virtually unknown in these savannas. The typical savanna trees are unarmed, evergreen, with large, simple, stiff, brittle, coriaceous leaves. The leaves of *Curatella americana*, one of the commonest species, measure 8″ x 5″ and those of *Byrsonima crassifolia* 4″ x 2″. A felty or hairy covering on one or both faces of the leaf is a very common feature, or else they may be markedly roughened, or waxy. The leaves droop and are not directly exposed to the sun so that even when the trees grow closely together, they cast little or no shade. The buds are seldom protected by scales as in the case of more extreme xerophytes. The root systems of these trees are superficial and feebly developed, the roots being long and rambling, but few.

It is a disputable point whether the savanna trees should be considered evergreen or deciduous. Warming, followed later by Bouillenne, held that they are deciduous because individual leaves live only 12 months, and are shed annually. Other authors have held that the trees are evergreen and that general leaf fall only occurs as a result of a fire. With this view the present writer is inclined to agree. By deciduousness, as applied to tropical vegetation, we should understand a relatively prolonged period of complete or partial leaf-fall coincidental with dry weather. It is true that many trees shed all their leaves annually not necessarily in dry weather, and put out a new crop immediately or after a short period in which flowering or fruiting may take place. Such plants are generally common in forests under mildly seasonal climatic conditions. They are certainly deciduous in a sense, but not in the sense of those trees growing under severely seasonal conditions which stand bare for months. Savanna trees may belong to the former category but they certainly do not belong to the latter. In the height of a dry season one may pass from a parched, leafless forest to an adjoining savanna and, if there has not yet been a fire, find every leaf intact. Once fire passes the leaves on the smaller trees are withered and fall, but in the writer's experience the trees never stand bare in the absence of this and must be considered evergreen.

Palm Savanna comprises a scattered growth of palms. It is very rare for both palms and trees to occur together. Sometimes the palms congregate to form "witches' rings" but almost always they occur singly and evenly scattered across the savanna. As with trees their density varies, and height depends on the species. *Copernicia tectorum*, where the writer saw it in Venezuela, never exceeded 6 ft. in height. In Cuba 60 ft. is exceeded by some species, while others are dwarfs, and do not exceed 18 in. Palms forming dense groves are not to be included in savanna. *Mauritia flexuosa*, for example, where it congregates as a gallery forest in the Venezuelan llanos constitutes a swamp formation and only takes part in savanna when it occurs scattered singly over grass. Savanna palms are typically of the fan-leaved type. Pinnate palms occur very rarely indeed and then, it seems, only under marginal conditions. The leaves of *Copernicia cerifera* are very richly coated with wax. Some of the Cuban palms have curious bottle-shaped swellings on their trunk. Where there is clay-pan, palm roots seem able to penetrate it and to survive adequately the poorly aerated conditions.

Pine Savanna is perhaps only a variant of Orchard and occurs in the limited area of tropical America where *Pinus* is present. Scattered pine trees of erect form and up to 60 ft. in height occur in the grassland, often mixed with orchard species of trees.

The physiognomy of the herb stratum varies but little with the changes in the tree layer. Very many variations in the grass associations do occur but not necessarily in keeping with variations in the trees. The grass is frequently shorter and less tufted with a higher proportion of sedges in palm savanna than in orchard.

The savanna flora exhibits a number of peculiar features. Compared with forest types the flora is poor in species and is apparently at its richest on the Brazilian plateau. At Lagoa Santa Warming found over 800 species on the savanna, while for the Mesa de Guanipa, Pittier listed only 109. While Pittier's list probably does not represent so exhaustive a search, it remains true that the Orinoco-Guiana savannas are poorer in species. A rich flora is, however, again encountered in the savannas of Cuba. An extremely small number of plant species occur in both savanna and forest, the floristic boundary between the two being as sharp as the physical. Everywhere in the Americas the transition from forest to savanna is abrupt, and there is seldom more than a transitional zone two or three yards in width. For-

TABLE 2. Composition of Local Communities in Tall Bunch-Grass Savanna.

Locality	Phase	Trees	General Herbaceous dominants	Variant dominants on river flats or depressions
TRINIDAD				
Erin	Orchard	*Curatella, Byrsonima, Miconia*	*Axonopus anceps, Trachypogon ligularis*	
Piarco	do	do	*Paspalum pulchellum, Leptocoryphium lanatum*	*Leersia hexandra Paspalum densum*
St. Joseph	do	do	*Trachypogon ligularis, Arundinella, Thrasya*	
VENEZUELAN LLANOS				
Mesa de Guanipa	Orchard	*Curatella, Byrsonima, Bowdichia, Roupala*	*Trachypogon* spp. *Axonopus chrysodactylus*	*Mesosetum chaseae, Paspalum* spp. *Sporobolus indicus*
Calabozo-San Fernando	do	do	*Cymbopogon rufus Andropogon condensatus*	*Sporobolus indicus, Steirachne diandra*
	Palm	*Copernicia tectorum*	?	
WEST INDIES				
Hispaniola	Open	None	*Themeda quadrivalvis*	
	Orchard	*Curatella, Byrsonima, Anacardium*		*Themeda*
	Pine	*Pinus occidentalis*	*Andropogon*	
Cuba	Pine Orchard	*Pinus* spp. *Quercus, Curatella, Byrsonima, Anarcardium, Tabebuia, Brya*	*Andropogon virginicus, Andropogon, Sporobolus, Panicum, Paspalum, Leptocoryphium*	*Andropogon virginicus*
	Palm	*Sabal, Copernicia, Acoelorraphe, Colpothrinax*	do (?)	
GUIANA LOWLANDS				
Venezuelan	Orchard	*Curatella, Byrsonima, Bowdichia*	?	
British	do	do	*Trachypogon plumosus, Axonopus, Andropogon, Aristida*	
Dutch	do	do	*Trachypogon plumosos, Gymnopogon foliosus.*	
French	do	do	*Trachypogon plumosus, Aristida, Axopus, Panicum*	
GUIANA HIGHLANDS				
Gran Sabana	Open	None	*Trachypogon plumosus, Paspalum contractum*	*Sporobolus indicus*
Rupununi	Orchard	*Curatella, Byrsonima, Bowdichia, Anacardium*	*Trachypogon plumosus, Aristida, Axonopus, Andropogon*	do
Amazon Basin	Orchard	*Qualea, Anacardium,*	*Paspalum, Andropogon, Sporobolus*	
BRAZILIAN PLATEAU				
Lagoa Santa	Orchard	*Bowdichia, Qualea*	*Trachypogon macroglossus Aristida tincta*	
Bolivia	Orchard	*Curatella, Tabebuia*	?	

est trees rise at the very edge of the savanna, their branches overhanging the grassland. Where forest and savanna country mingles, each type occurs as pure patches surrounded by the other, the forest as "islands" in the savanna, the savanna as "lakes" in the forest. Only in the short bunch-grass type of savannas is there anything like a mingling of forest and savanna elements. Forest trees never occur in tall bunch-grass savanna and savanna trees are never found in forest. The savanna grasses are morphologically different from forest grasses and the two do not interchange. Occasional clumps of savanna grass may be found in other low, open forest or bush communities such as the "muri-muri bush" and that is all. Such plants as are found both in high forest and savanna are mostly forbs or climbers.

The principal genera to which savanna grasses belong are: *Trachypogon, Paspalum, Panicum, Andropogon, Axonopus, Arundinella, Sporobolus, Thrasya, Leptocoryphium, Setaria, Mesosetum, Sacciolepsis, Cymbopogon, Steirachne, Aristida, Eragrotis, Sorghastrum, Cipella, Gymnopogon, Clitoria, Cenchrus, Chloris, Ctenium.* In one locality in Haiti, Themeda is dominant but this appears to be essentially a subtropical element: it is further stated to be a sod-grass rather than a bunch-grass.

Sedges belong mainly to *Rhynchospora, Scleria* and *Bulbostylis* (*Scirpus*) also *Dichromena, Stenophyllus* and *Fimbristylis.*

Forbs belong mostly to the families Compositae, Leguminosae,, Convolvulaceae, Malvaceae and Polygalaceae.

Shrubs are most commonly Miconia and other genera of the Melastomaceae. Others noteworthy are *Byrsonima verbascifolia, Palicourea rigida, Pavonia speciosa,* all of which are quite widespread. Among palms, the principal genus is *Copernicia.* Others are *Acoelorraphe, Colpothrinax, Coccothrinax, Mauritia* and *Sabal.*

Trees do not belong to any particular families: some are localized and some very widespread. *Curatella americana* and *Byrsonima crassifolia* are almost invariably present throughout. *Anacardium occidentale, Bowdichia virgilioides, Roupala* spp., other *Byrsonima* spp. and *Xylopia grandiflora* are very widespread. The principal Brazilian elements are *Qualea grandiflora, Hancornia speciosa, Plathymenia reticulata, Salvertia convallariodora* and *Vochysia ferruginea.* Cuban species are *Brya ebenus, Tabebuia lepidophylla, Rondeletia correifolia, Malpighia glabra* and *Quercus virginiana.* The pines in Cuban savannas are *Pinus tropicalis, P. caribaea* and *P. cubensis.*

There is insufficient information at present to delimit plant associations, but the accompanying table shows the dominant species of the best-known areas. Dominance among the grasses seems to vary fairly rapidly from place to place and few of the known localities show exactly the same composition. *Trachypogon plumosus* is generally dominant all over Guiana, both on the highlands and lowlands.

Trachypogon ligularis occupies much the same position for Trinidad and the eastern llanos, *T. macroglossus* for the Brazilian plateau. It may in fact be possible to speak generally of a Trachypogon-Aristida association for the savannas on the South American mainland. *Sporobolus indicus* is another widespread dominant, generally on the lower-lying ground

Among the trees, Curatella and Byrsonima are widespread to an astonishing degree, from Cuba to South Brazil, a range of some 3,000 mi. Other species are localized. The whole flora embraces elements of all degrees of distribution from the most localized endemics to general species of the wide range of Curatella. Most of the savanna plants may be considered specialized in some manner.

SEDGE SAVANNA

As has been seen, sedges are always present in the Tall Bunch-Grass Savanna. In some of the wettest areas, where the rainfall is high or flooding prolonged, sedges become more abundant than grasses and a distinctive type of savanna is formed. There are, of course, many intermediate cases, but when fully developed, the Sedge Savanna is quite distinctive. It occupies only relatively limited areas, and is principally typified by the Aripo group of savannas in Trinidad and many of the coastal savannas of Surinam and French Guiana. Elsewhere it occupies the swampy depressions on the Guiana plateau. We hear of it on the Amazon (Spruce 1908) and it was described by Williams (1940) on the Paragua River in Venezuela and by Charter (1941) in British Honduras. Of all the savannas this approaches closest to swamp in type of plant growth and habitat, and has been regarded as swamp by some writers (Marshall 1934), but it is distinguished by the xeromorphic structure of the dominant plants and by the seasonal desiccation of the ground, swamp soil being by definition perpetually wet.

The dominant herbaceous stratum is shorter than in the Bunch-Grass Savanna, but the plants are not so well tufted and a greater proportion of the soil is covered. Sedges are predominant, and grasses relatively rare. There are many small herbs, including terrestrial orchids and, typically, Drosera and Utricularia; also Lycopodium and many ferns, while a spongy moss covers most of the soil between these plants. Some of the dominant sedges may attain a height of 18 in. and their inflorescences 3 ft. at flowering, but most of the plants are only 6 to 9 in. in height. The plants are either weakly or not at all tufted and raised tussocks are not formed.

Many small hygrophilous plants are present but the dominant sedges and grasses are xeromorphic in structure with narrow, harsh leaves, flat or rolled, cutting or pilose. The type of sedge with broad and flat or triangular, pith-filled leaves is not present. The herbs have most of them underground perennating organs. In Trinidad, the plants have a short vegetative period at the beginning of the rainy season

after the soil is moistened and before it becomes waterlogged. In Surinam, according to Lanjouw (1936) the vegetative period is at the end of the rains.

Scattered small shrubs or palms are generally present, the shrubs only 2-3 ft. high and generally some 20 ft. apart. They do not adopt any special gnarled form, bark is generally thin and leaves smaller than those of savanna trees such as Curatella, generally about 2″ by 1″. The shrubs are unarmed and evergreen, their leaves simple, coriaceous, entire, generally waxy, sometimes felty or hairy.

Dominant sedges belong to the genera *Lagenocarpus, Rhynchospora, Bulbostylis,* and *Scleria. Leersia hexandra* is generally present, and many other grasses typical of bunch-grass savanna occur sporadically. Shrubs vary: in Trinidad and the Guianas, Chrysobalanus, Byrsonima, Ilex, Miconia; in Venezuela (Williams 1940) *Duroia sprucei* and *Erythrina glauca;* and in British Honduras (Charter 1941) *Crescentia cujete* and *Cameraria belizensis.* In British Honduras the palm *Acoelorraphe wrightii* is present, and in Guiana, Mauritia occurs locally.

Another feature of the sedge savanna is its tendency to occupy relatively small patches alternating rapidly with forest and woodland of a specialized kind and forming a mosaic. This tendency is first remarked in the tall bunch-grass savanna of wetter areas, where "bush islands," inclusions of the local forest, may become common. In the sedge savanna the dispersion and intermixture of savanna and woodland becomes extreme and the woody communities more specialized.

SHORT BUNCH-GRASS SAVANNA

This name should only be tentatively applied at present in tropical America as we have, unfortunately, insufficient detailed information about the communities to which it may pertain. In Africa, the short bunch-grass savannas, in Bews' account (1929) occur in areas of lower rainfall than the tall bunch grass, between limits of 20 and 35 in. per annum. The grasses reach only a height of one foot, and the trees are fewer and more xeromorphic, generally of the Acacia type.

We must certainly recognize that the savannas of the drier parts of tropical America, where the annual rainfall drops below 40 in. differ considerably from the pattern predominant elsewhere. Whether these are correctly worthy of the term short bunch-grass savanna it is difficult to say. On extending our knowledge we may have to allot some other name. For the present, however, the writer proposes the use of this term.

The principal feature of this type of savanna is that it does not form the vast, sweepingly monotonous expanses of tree-dotted grass typical of the tall bunch-grass type. It is essentially a component of an intricate mosaic of rapidly alternating communities of various kinds—low thorny bush, taller evergreen forest, palm groves, grassland with or without trees. In the well-watered parts the evergreen forest is common, in the drier parts we see more of the thorn bush and even patches of cactus. Each of the components of the mosaic is a distinct plant formation and they alternate rapidly according to slight changes in site factors. The savanna itself thus occupies only a portion of the ground.

The "Dry Savanna" of Haiti should probably be classified under this head, with its dominant grass *Uniola virgata* and accompaniment of Agave, Plumeria, Maytenus, Schaefferia and Jacquinia. Here also belong the *Paspalum bakeri* savannas of Barbuda surrounded by Bucida trees, disposed as pockets in Bushland. In Cuba, on a part of the Trinidad plains near the coast, savanna of *Sporobolus indicus* dotted with small thorny trees (*Brya ebenus*) is mixed with local thickets of *Copernicia macroglossa, Acacia farnesiana,* prickly pears and tall cacti. The writer's observation of Acacia thickets in the savannas of Venezuela south of the Orinoco may be taken to indicate an approach to these similar conditions.

In the extreme south the chaco vegetation (*Parque chaqueño*) appears to include short bunch-grass savanna intermingled with thorny thickets and with low evergreen forest and cactus scrub, as well as with swamp communities such as herbaceous swamps and palm groves. On the borders of the arid zone of the Brazilian north-east in the state of Ceará, there are flat plains with a vegetation very similar to that of the Chaco, both floristically and ecologically. It seems probable also that the *campos mimosos* of the São Francisco valley which likewise border upon the arid north-east should be so classified.

HIGH-GRASS SAVANNA

Even with the aid of Bew's qualifications that the important criterion is not so much the height of the grasses as their hygrophilous character, it is difficult to find any very convincing examples of this type of savanna in America. In Africa, according to Bews, it consists of tall, coarse grasses 5 to 15 ft. in height and occurs either around forest margins or over wider areas where forests have been destroyed. The community depends on fire for its maintenance. The forest margin type of habitat is limited in area and examples are afforded by the appearance of Scleria and Imperata forming a taller growth at the borders of savannas—Trinidad and elsewhere. Schomburgk (1847) mentioned very tall thickets of grass bordering the rivers in the Rupununi savanna area in places where there was no gallery forest, and this is doubtless another example, as are the numerous patches of tall grass on river banks everywhere, although these cannot be said to depend on fire for their maintenance. Perhaps they should be placed with Bews' "forest margin and hygrophilous types."

The degraded forest type of habitat is less common in America than in Africa since man and fire have had much less effect on the primaeval vegetation. In some intensively disturbed areas there are certainly grasslands which have supplanted forests in historical times and these are of three kinds. The

first, typified by the Gran Sabana and the Venezuelan mountains, differs scarcely, if at all, from the general type of tall bunch-brass savanna. The second is typified by the "fire savannas" of the northern plain of Trinidad with Imperata, Arundinella, Andropogon and Maximiliana palms. The grasses here are only slightly taller than those of the tall bunch-grass savanna and include species of the latter. Thirdly, there are grazing lands like those of Antigua and Cuba, whose African appearance was commented on by Marie-Victorin and Léon (1942-44). These are floored with soft grasses, which grow tall if ungrazed, and covered with flat-topped leguminous trees.

In none of these cases do the grasses at all approximate to the height of the African high grasses. There is, however, one example which must be quoted where really tall grass is involved, the low flood-plains of the middle Orinoco, where Myers (1933) was confident that he had found true high-grass savanna. On first reading his account, the writer was inclined to agree with him. The vast expanses of *Paspalum fasciculatum* as high as a man are suggestive, though the obviously swampy habitat of the *esteros,* under deep water for much of the year, would be difficult to reconcile. Acquaintance with the *campos de varzea* of the Amazon (Bouillenne 1930), with their *Paspalum amplexicaule* and *P. spectabile,* throws the Venezuelan community into its true perspective. Clearly both phenomena are the same and the type that Myers found is not high-grass savanna at all, but swamp grass, the same phase of Herbaceous Swamp as the *campos de varzea* represent, and a very different ecological proposition.

On the whole it cannot be said that the evidence in favor of recognizing high-grass savanna in tropical America is very strong. We could say that certain man-induced grasslands are equivalent to the African high-grass savanna, or resemble it ecologically. The influence of man in this connection will be discussed further under Habitat.

Habitat

Climate

In discussing the savanna in relation to climate, we must distinguish between the microclimate of the savanna itself and the macro- or regional climate to which both the savanna and any forests of the vicinity are subjected. A dense tree cover exerts such a profoundly modifying effect that the microclimates of adjacent savanna and forest must be radically different, but such variations are the result of differences in the plant cover and cannot be said to have any major controlling influence upon it. If we are to examine the contention, supported by so many eminent authors, that the savanna is a climatic formation, then it is the macroclimate which must receive closest scrutiny and we must be able to define the typical savanna climate in terms of rainfall, temperature and so on.

It will be clear from the outset that the savannas are found under a great variety of regional climates and are juxtaposed with a variety of forest types.

Temperatures are essentially similar throughout, averaging between 65° F and 80° F "in the shade" —of which, actually, there is none in the savanna. Temperatures of surfaces exposed to the sun are of course rather higher. For the Guiana plateau Schomburgk mentioned figures of about 120° F. There is little seasonal variation in temperature and frost is unknown. No savannas occur at altitudes where temperatures become effectively low. It therefore seems wrong to speak of a "winter" season in the savannas as some writers have done. It is perhaps difficult for a person accustomed to temperate conditions to realize that there is no winter in the lowland tropics in the sense of a season in which temperatures become effectively lowered. The tropical year is divided into one or two relatively hot *dry* seasons alternating with one or two relatively cool *rainy* seasons (actual temperature differences are slight) and in Latin America it is customary to refer to the former as *verano, verão,* "summer," and to the latter as *invierno, inverno,* "winter," by analogy from the Iberian peninsula with its hot, dry summer and cold, wet winter. However, this is not a scientifically correct practice since the "summer" and "winter" do not necessarily coincide with the solar seasons. In Venezuela, for example, the *verano* is from January to May, in the late winter and spring of the solar season! We cannot admit that the "dry, cool winters" regarded by Schimper, Warming and others as characteristic of the savanna climate represent a correct interpretation of the facts.

Rainfall is the all-important climatic factor in the tropics and the vegetation everywhere shows important responses to variations in the amount and distribution of it. Rain forests are found where drought periods are insignificant and increasing xerophytism becomes apparent with greater incidence of drought periods. Drought becomes felt whenever evaporation exceeds precipitation for long enough to begin to dry out the soil and a number of students of this question (Charter 1941, Mohr 1944, Hardy 1946, Beard 1946) have concluded that drought periods in the moist tropics can be said to occur whenever the monthly rainfall fails to attain 4 in. in a month. One or two months with less than 4 in. will not perhaps be perceptible unless quite or almost rainless, but three, five or more drought months are bound to be effective and where they occur regularly at definite seasons the vegetation shows xeromorphic characters.

The savannas are subject to a wide range of rainfall conditions, which is reflected in the accompanying distribution of the three savanna types, sedge, tall bunch-grass and short bunch-grass. Some of the wettest conditions are experienced at the Aripo savannas of Trinidad and the Guiana coastlands from British Guiana to the Amazon mouths. Here the average rainfall is everywhere over 80 in. a year and ranges locally to a recorded maximum of 140 in. (*fide*

Benoist) in French Guiana. Drought months are normally three or less each year and there are still at least 2 in. of rain during each of those months. Associated forests are rain forests for the most part. In such areas savannas are very commonly of the sedge type or, if not, of the tall bunch-grass type with a high proportion of sedges. The greater proportion of American savannas lie in rainfall zones of between 50 and 65 in. per annum with five drought months in a year. Absolutely rainless months are extremely rare anywhere and a few showers continue to fall in the driest weather. The Gran Sabana is a slightly moister area with 65-70 in. of rain and three drought months, the eastern Venezuelan llanos are a drier area with 40-45 in. and seven drought months. Within the above limits, the tall bunch-grass savanna reaches its optimum development, alongside seasonal forests. Savannas continue to be found in the limited semi-arid regions of tropical America, in the Brazilian north-east with 30-40 in. of rain and in the Chaco with its 35-50 in. which drop locally to only 20 in.: in such areas, distribution of rain is irregular and long droughts are liable to occur. Savanna here is of the short bunch-grass type, and associated woody growth is thorn bush and cactus.

What then constitutes the typical savanna climate? In what way do savanna and forest climates differ? We have seen that savannas and forests exist side by side under rainfalls varying from 20 in. a year to 140 in. and that over this range there is a variation in life-forms in both savanna and forest from short bunch-grass to sedge and from thorn bush to rain forest. It is substantially the view of most writers concerned that a long, severe dry season characterizes the savanna climate. According to Warming (1892) this is generally true, in wetter regions some unfavorable soil factor being present to depress moisture supply. In Schimper's view (1903) a dry, cool winter would be equivalent to a long rainless season and savanna would be further favored by frequent, even if weak, precipitation during the vegetative period of the grasses. Hayek (1926) stated that savanna would be widespread where the bulk of rainfall falls during the vegetative period of grasses, a curious inversion of cause and effect: for in the tropics, where there is no winter, properly speaking, the vegetative period of grasses will naturally coincide with the rainy season, whenever that is. This period is not fixed but is conditioned by the prevailing climate, moreover rain at any season favors trees as much as grasses. We fall back, essentially, on the supposition that a severe annual dry season climatically favors grassland. The great range of rainfall conditions demonstrated above under which savannas occur does not necessarily exclude the possibility of a typical savanna climate, if this is a very dry one, since some adverse edaphic factor may be present in the moister areas to depress the availability of moisture down to a level equivalent to that afforded by a drier climate. We have merely to enquire whether there is any climate which will cause the appearance of savanna in the absence of fire or any adverse edaphic conditions.

We are bound to conclude that there is not. Meteorological data available to us today show that former inferences of the long, rainless dry seasons in the Venezuelan llanos and elsewhere were not factually correct. The average savanna climate is not as dry as used to be believed and in the really dry and semi-arid regions, savannas become less and not more conspicuous. Where there are less than 40 in. of rain a year savannas become restricted to relatively small patches mixed with xeromorphic bush and with under 20 in. grassland disappears altogether. The typical vegetation of the arid regions of tropical America is thorn woodland and cactus scrub, formations of which grasses are insignificant components. Even if we suppose that a forest type growing under a rainfall of say 60 in. is occupying a moister site, due to some soil factor, than the savanna alongside it, we should also expect to find the savanna occurring on optimum sites under lower rainfall elsewhere but we do not: we still find woody growth, only of a more highly xeromorphic character than before. There is no climate on record under which there is savanna on optimum sites. In a previous work (1944) the writer described a series of "seasonal" plant formations showing progressive reduction in stature and forms from rain forest to desert and corresponding to progressive increase in the incidence of the drought factor. Savanna has no place in this series and all the formations are woody. Evergreen, semi-evergreen and deciduous seasonal forest lead on in descending series to thorn woodland, cactus scrub and so to desert. These are all essentially climatic formations and the only way in which we could envisage savanna as a climatic formation would be to insert it in the series between deciduous seasonal forest and thorn woodland, which is theoretically inadmissible because thorn woodland is a less reduced type than the savanna and because savanna life forms show xeromorphy of a different order from that of seasonal forests and thorn woodland. The writer concluded (1944) that "the tropical grassland climate simply does not exist" and wishes to reaffirm that conclusion here.

Due to the difference in microclimate, the savanna is of much drier appearance than forest at any time of the year and this probably led early observers, who had few or no meteorological records for study and who saw the broad regions of savanna rather than the localities where savanna and forest mingle, to the conclusion that the savanna must represent a drier regional climate. Later this became a fixed idea so that a modern observer like Bouillenne (1930) was constrained to advance a quite fantastic theory in support of it. Meteorological observations made in Trinidad (Brooks 1936) in the forest and in the open showed very great differences in temperature ranges and humidity. Sun and wind get to the soil and a savanna dries out after rains more quickly than forest. It must be appreciated, however, that this drier microclimate is not a cause but an effect, due to preexisting vegetative cover. If all

factors other than the microclimate favored the growth of forest, succession would take place and the microclimate become ameliorated. This is what happens when forest is cut down and the soil bared.

Savanna vegetation is of xeromorphic order partly in response to the microclimate—excessive insolation and drying winds—but principally because, as will be shown later, the habitat is physiologically dry. The life forms of savanna trees and herbs, it may be noted, differ radically from those typical of seasonally dry forests and woodlands—deciduousness, microphylly, spinescence, stem and leaf succulence and water storage tissue. The savanna grasses were shown by Bews (1929) to be highly developed and specialized and they represent a life form closely adapted to the savanna habitat but rarely seen in seasonal forests and woodlands.

In summary:

(a) Savannas occur under a variety of climatic conditions, from an annual rainfall of 20 in. with over 7 drought months up to over 100 in. with negligible drought periods.

(b) Under rainfalls between 20 and 40 in. short bunch-grass savanna is found, tall bunch-grass between 40 and 80 in., while sedge savannas become very common with more than 80 in.

(c) All the climates, given suitable soil conditions, can and do support forest or woody vegetation of some kind.

(d) The driest climates in tropical America support thorn woodland, cactus scrub or desert, never savanna.

(e) Savanna life forms indicate a response to edaphic conditions rather than to climate.

(f) There is no such thing as a tropical grassland climate, and it therefore follows that the savanna is an edaphic or biotic formation.

TOPOGRAPHY

There is a relation between the savanna and its landscape, so compelling that Lanjouw (1936) began his definition of the plant formation: "Savannas are plains. . . ." This is generally, if not always strictly literally, correct. Savannas occur at any altitude from sea level up to 4,000 ft. above it, their highest point being on the Gran Sabana. They are absent from the Andine mountain chains. Geologically, they overlie a great variety of rock types, and the nature of the parent rock is not significant. Certain rocks, notably serpentine, seem predisposed to an association with savanna but no absolute correlations can be made. A study of geomorphology, however, gives us interesting evidence. In the majority of cases, savannas are seen to occupy very gently undulating country. Very frequently the land is level or almost so: rarely, it is sharply undulating and in a very few cases mountainous. Often, where there are savannas in broken country, they are patchy and cling to flat surfaces at the top or foot of the steeper slopes. Savannas are predominantly associated with plains, terraces or plateaus.

All this is capable of a geomorphological interpretation. As far as the writer is aware, the study of land forms has not hitherto been invoked to any important extent in the elucidation of plant ecological problems in tropical America. It is worthy that it should be, and in this particular case it is indispensable. Land form has an important influence on the plant habitat, not only as the present and actual configuration of the ground surface which determines external soil drainage, rate of water run-off, predisposition to flooding and so on. Past history and the evolution of the present landscape are also important because of the soil-forming processes which may have taken place. Soil development owes much to topography; in fact in its more advanced stages it may be said to owe everything to this. In studying plant formations, therefore, which are associated with special soil conditions the land form must be taken into consideration as a soil-forming factor. (Ref. Milne's work in East Africa: 1937, 1941.)

Land form is the product of a series of constructive and destructive cycles, of a continual building up and tearing down. A constructive phase will occur when land is built up from the sea floor by the emission of ashes and lava from volcanoes, or alternatively, by the deposition of sedimentary strata beneath the sea, followed by their uplift and exposure. Such newly formed, young landscapes are flat and featureless, undissected and without regular drainage channels. Their soils also are young and undeveloped. As soon as a new land surface is exposed to the atmosphere, however, a destructive phase sets in, and after a shorter or longer period the surface becomes deeply dissected by drainage channels, broken up into ridges and valleys whose depth will depend upon the degree of uplift to which the young surface was subjected, and to the amount of the rainfall. Generally, the higher the rainfall the steeper the erosion slopes. On such mature, diversified topography soils develope to some, but not to their greatest, extent. Finally, the land is reduced to lower and lower outline and in extreme old age is once again flat and featureless, undissected and without regular drainage channels. The soils in this case are very highly developed because there has been a long period without either erosion or aggradation at the surface, and the fullest extent of weathering and translocation of materials takes place, usually under the influence of ground water due to the flatness of the site.

It will be found that in almost all cases savannas cover senile topography, either old alluvial plains or ancient highlands on which an old-age topography has developed. North of the Orinoco and the West Indies and Central America the savannas occur for the most part upon plains of Quaternary alluvia whose formation has been long since completed but which are not yet beeing subjected to destructive erosion. In a sense, these are still young landforms, not having passed through a destructive cycle since their formation. This has been due solely to lack of uplift and they have in effect passed directly from

youth to old age. As will be seen, highly mature soils have developed upon them. This type of landform is seen also in lowland Guiana and in Bolivia and Paraguay, but on the Guiana and Brazilian highlands the savannas occupy peneplaned stretches of the uplands, plateaus where a temporary base level of erosion has been reached and where, again, highly mature soils have developed. In a few cases, as on Barbuda Island, savannas are found on very young sites, and here the lack of soil and landscape development is found to lead to similar effects on soil moisture and drainage as the well-matured development of senile landscapes.

In summary:

(a) Savannas occur upon ill-drained country of little relief.

(b) Most generally this is the product of a senile landscape where there is no longer much aggradation or erosion, where surface drainage is slow due to lack of slope and of organized drainage channels, and where highly mature soils have had time to develop.

(c) Less commonly, the necessary conditions occur on country which is geomorphologically young.

(d) Savannas are never associated with young alluvia nor with uplands in a juvenile or mature stage which have steep erosion slopes and rapid drainage.

SOILS

Detailed soil investigations in savannas have been few and only cover areas in Cuba, British Honduras, Trinidad, British Guiana and the Gran Sabana in Venezuela. For other parts one cannot, unfortunately, place too much reliance upon the casual observations of passing explorers and botanists since they are not trained observers where the soil is concerned and may stress insignificant or unimportant characters, overlooking the essential. Thus, the observation that "the soil is sandy" tells us little, for it only means that the surface soil is sandy. It may be sandy to considerable depth or change to clay below, and radically different soil types may be present. For an analysis of soil information it will be desirable to rely only on the specialized work.

It will be as well to inquire, to start with, what are the important characteristics of tropical soils as affecting the natural vegetation that grows upon them. In a study of the distribution of soil and forest types in south-central Trinidad in 1936, Hardy, Duthie & Rodrigues arrived at the conclusion that soil-moisture is the essential factor determining changes in vegetation and this is a function of climate, topography and the physical character of the soil. Within a single climatic area, for example, certain combinations of soil and topography may make for a moist habitat favoring an evergreen forest and other combinations for a dry habitat favoring a semi-evergreen or deciduous forest. The moisture-supplying ability of the soil is determined by its physical structure, that is, by its permeability, aeration, conductivity and retentivity of moisture. Soils that are too freely drained, too porous and permeable, will be physically dry. Soils that are too poorly drained internally, too compact, impermeable and badly aerated, will be physiologically dry. The chemical constitution of the soil was found by Hardy, Duthie & Rodrigues to have little or no influence upon natural vegetation types. A similar view was expressed by Charter (1941) for British Honduras and by Beard (1946) for Trinidad as a whole. A classification of the soil types of Trinidad based on their natural drainage was drawn up by Hardy (1940) and applied by Beard (1946) to the ecology of local vegetation types.

The present writer finds it very hard to subscribe to the view of what may be termed the "Dutch school" (Pulle, Ijzerman, and Lanjouw) that the savannas, being associated with excessively leached soil, have originated as a result of the leaching process. This view implies that soils deficient in mineral nutrients are unable to support a luxuriant forest growth, a proposition which does not appear to the writer to be in accord with the facts. A very fine rain forest at least 120 ft. tall is found in British Guiana on expanses of deep, white, quartz sand whose inherent fertility is extremely low and must be just as low as that of savanna soils. In view of his earlier work it is curious that Hardy (1945) went over to the Dutch school and supported their view that soils of inherently low fertility are only able to support "a poor sort of forest." As an example of this he cited the white sand rain-forests of British Guiana, but it is difficult to see on what ground these can be described as a "poor sort of forest." Physiognomically they are essentially the same as rain forests on any other kind of soil, differing only in composition and in minor structural features. Chemical analysis has certainly demonstrated the extremely low nutrient status of savanna soils and of their natural herbage as a stock-feed but a low nutrient status is typical of all mature soils of high rainfall areas in the tropics. Reference may be made to the analyses of forest and savanna soils at the Erin Savanna in Trinidad and in the Rupununi district of British Guiana, cited earlier in this work, which failed to disclose any effective chemical differences between the two. In Hardy's paper of 1936 with Duthie and Rodrigues he detected no differences in composition between forest growing on fertile marl and unfertile sand.

The writer cannot admit that under the climatic conditions affecting forest and savanna in tropical America the chemical constitution of the soil can have any influence upon their distribution, and maintains that the physical constitution of the soil, particularly as regards internal drainage, is the essential factor to be considered.

Bennett & Allison (1928) found in Cuba that savanna soils have special features of physical structure which distinguish them from forest soils, in fact, "the term savanna . . . carries both a vegetative and a soil meaning." As a general rule, the savanna soils in Cuba exhibit a permeable horizon overlying an

impermeable subsoil due to the presence of rock at a shallow depth or of a clay pan or iron pan. The majority of savanna soils elsewhere, of which we have accurate descriptions, are of this character and others are similar in their drainage relationships. On the basis of the data we have, it is possible to describe a number of typical savanna soil types to which all the known soils approximate more or less closely.

The first of these may be called the "sand-over-pan" soil, divisible into "sand-over-clay," "sand-over-rock" and "sand-over-ironstone" types. The profile takes the form of a black to grey, leached, light sand generally 9 to 12 in. in thickness overlying either a highly compact and impermeable red and white mottled clay, or a dense stratum of unweathered rock, or an accumulation of concretionary ironstone in the form of small pebbles and lumps, called *perdigón* in Cuba, or of massive conglomerate called *mocarrero*. Subsoil drainage is obstructed by a clay-pan or an iron-pan or by solid rock. The upper horizon is of variable thickness, sometimes two ft. thick or more, sometimes disappearing altogether so that the clay or ironstone appears at the surface. On low ground the sand is generally very dark in color, but on rolling ground where it may be subject to blowing by the wind it is generally lighter, grey or even pale yellow. The dark color appears to be due to the incorporation of fine charcoal, the residue of fires, rather than to humus, of which there is little. If dark at the surface it may often show bleached white at the base of the horizon. This upper horizon varies in texture from sand to silt or loam but is always typically light. Ironstone concretions may be present. Transition to the underlying impermeable horizon is generally fairly abrupt. This may consist of unweathered rock of various types—chalk, sandstone, serpentine, gabbro—or of that red clay which is the typical end-product of rock weathering in the humid tropics.

The clay may be stoneless or nearly so, or may contain gravel or rotten rock or bands or lumps of ironstone. It is predominantly red in color but on closer inspection will be found to contain brilliant mottlings of red, yellow and white. It becomes a whitish clay with red mottlings at greater depth. The mottling indicates seasonal waterlogging. Where iron-pan is present it may be composed of lumps and pebbles of ironstone or of a solid band up to several inches thick. It generally caps a red-mottled whitish clay similar to the subsoil of the clay-pan type. The essential feature of these "sand-over-pan" soils is the superposition of a light-textured horizon upon a heavy, impermeable one. Such soils underlie almost all the savannas of Cuba, British Honduras and Trinidad.

On the eastern Venezuelan llanos and much of the Guiana plateau these same soils occupy the low ground, while knolls and rises feature the second general soil type which we may describe and name the "clay with ironstone" soil. This soil has evidently been derived by erosion from the "sand-over-pan" type, for it is based upon the same red clay which appears in the rising ground, either naked or capped with a superficial layer of ironstone. The sand horizon has been removed, leaving bare clay, or a layer of gravel upon the surface, or even, locally, a bed of ironstone conglomerate. Bare clay is dark and almost black at the surface, hard and impermeable. At a depth of a few inches iron concretions may be present, and it merges quickly into the usual red and white mottled clay. The stone layer, where present, varies greatly in thickness from the occasional pebble to beds a foot thick. It is composed mainly of ironstone nodules, but quartz and granite fragments are also seen locally. Little herbage grows where the stones are thick. Warming mentions this soil in the south Brazilian savannas.

A third and much less common type of savanna soil we may name the "clay flat" soil. This was typical of the part of the Gran Sabana visited by the writer and also occurs at the Aripo savannas in Trinidad and in some parts of Cuba. Here the soil consists of a pale-grey clay or silty clay at the surface, merging below into a pink or red and white mottled clay which may contain ironstone concretions. The surface clay is very hard and compact and impermeable, and seems not to be of the type which shrinks markedly or cracks when dry. In some cases such a clay soil is found overlying rock at shallow depth, as in the case of the Barbuda savannas and of the Holguin and Camagüey soils in Cuba. Soils of this type commonly occupy very flat ground or even depressions.

Finally, and rarely, there are "deep sand" soils, typified by the Norfolk fine sand of Cuba and the soils of some lowland Guiana savannas. These are deep, loose, grey or brown sands merging downwards into grey, yellow or red-brown sand or sandy loam. There is little difference in texture between the horizons and there seem to be no obstacles to downward percolation. These soils occur on areas of low relief, however, presumably with a high water table at certain seasons when stagnant ground water will be present.

"Hogwallow structure" is characteristic of the soils which are sandy at the surface when they occur on level ground. Undulating areas do not exhibit this phenomenon, nor flats where the surface sand is loose and windblown. Heavy topsoils exhibit it to only a limited extent. It takes the form of a marked unevenness of the surface which is broken up into steep-sided hummocks and depressions, generally about 12 to 18 in. across and 9 to 12 in. deep, sometimes more. Some of the depressions are more or less connected and resemble meandering drainage channels, others are not. They become pools of standing water in rainy weather. Hog-wallow structure is not a feature solely of savannas but occurs also under forests where these are growing on senile flat topography. The writer has never seen a satisfactory explanation advanced to account for the formation of these odd hummocks and depressions, and is unable to suggest one.

The lack of pronounced relief which is characteristic of savanna lands accentuates any tendency to imperfect drainage within the soil. For a soil to remain well-drained and aerated, surplus water must be fairly rapidly disposed of by either downward percolation or surface run-off or both. Otherwise, there will be an accumulation of water, particularly under heavy rainfall conditions, leading to waterlogging or even inundation. Impervious soils can occur on broken ground without becoming waterlogged, and porous soils on flats if percolation is sufficiently rapid and the water-table sufficiently deep. Where, however, there is a combination of heavy rains, flat country without a regular system of drainage channels and impermeable subsoils, then the tendency to waterlog will be strongly accentuated. Even porous, sandy soils on flats may be equally prone to this if the water table is high and the rain heavy and prolonged, and one suspects that this occurs in the case of the "deep sand" savanna soils. In accounts of savannas everywhere in the Americas we read over and over again that they are under water for long periods during the rainy season. The flood water is seldom deep, or seldom remains deep for long. Generally, water stands in shallow pools, or fills the hogwallow channels or soaks the surface soil to a boggy consistency. Where deep water collects for long the typical savanna disappears in favor of swamp vegetation.

A water-table in the correct sense can only exist in the "deep sand" type of savanna soils. Strongly impermeable subsoils, whether clay, rock or ironstone, do not permit the existence of a watertable, properly speaking. To those familiar with conditions in the temperate zone, some of the properties of tropical clays may appear astonishing and it may be hard to realize that many of them, particularly those which are most highly weathered, consist of over 90% of clay particles with a very minute proportion of pore spaces and can be almost as impermeable as a solid sheet of rock. Even when the surface has been waterlogged for a long time such soils may be relatively dry at a depth of several feet. The only type of water-table which one can associate with such a soil is a "perched" one, and that will only exist during the rainy season, disappearing altogether during drought.

Forest soils are distinguished from savanna soils in important respects of their natural drainage. Upland (as distinct from swamp) forests occur always on soils which are relatively well-drained either internally or externally or both. Such forests typically cover broken country with well-drained slopes and juvenile soils. Soils of the "sand-over-pan" type can sometimes be found under forests, but the ground will be sufficiently sloping and well supplied with drainage channels to preserve a well-aerated top soil.

The "clay with ironstone" type is never found under forests, in the writer's experience. Pure clays and deep sands are of course common as forest soils and the former may be based upon the same red and white mottled clay as savanna soils, but will show important differences at the surface. Forest clays are dark brown at the surface and of good crumb structure, both features showing the incorporation of humus. Tree roots penetrate deeply. In dry weather the clay shrinks and cracks deeply, permitting aeration of the deeper layers. Some forest soils are very shallow, with sand or clay over rock. Sometimes there is virtually no soil at all, forest of magnificent aspect continuing to grow upon a mass of stones. Such country will be steeply sloping or otherwise well drained. Specialized swamp forests occur on soils, generally young alluvia, which are ill-drained due to low relief but where the ground water does not become stagnant and deficient in oxygen. Such, for example, are the *igapo* and *varzea* forests of the Amazon, flooded for all or part of the year. True water tables exist in these soils, oscillating with the seasons.

In summary:

(a) Natural drainage is the most important characteristic of tropical soils which affects the distribution of vegetation types such as forest and savanna.

(b) The chemical composition of the soil has little or no influence upon such distribution, and it is not true that infertile soils can only support an impoverished vegetation.

(c) Savanna soils differ from forest soils in possessing features which, in interaction with topography and rainfall, affect their natural drainage unfavorably.

(d) These savanna soils in the majority of cases exhibit the superposition of a permeable horizon upon an impermeable. They may consist also of heavy, impermeable clays or porous sands, in areas of low relief.

(e) The savanna soils have, typically, no true water table. A perched water table exists intermittently during wet weather.

(f) The surface in savannas is waterlogged or flooded for periods during the rainy seasons and alternately dried out. Ground water may become stagnant.

(g) The soils of upland forests are well-drained by virtue either of their porosity or of sloping ground.

(h) Specialized swamp forests occur on ground subject to perpetual or periodic inundation but the water does not become stagnant.

BIOTIC FACTORS

One of the most arresting differences between the grasslands of the American and African tropics is the total lack on the former of a natural population of grazing animals, such as is so abundant in Africa. The great herds of ruminants and the carnivores which prey upon them, roaming the open grassy country by the hundreds and thousands, are an African phenomenon. All the mammals and marsupials of lowland tropical America are forest animals. South American forests are reasonably well populated with animals, for example the tapir and

peccary, deer, armadillo and rodents such as the capybara and agouti, together with some carnivores, notably the jaguar and puma. Where savannas exist side by side with large areas of forest these animals often move onto the savannas and may be hunted there, but their home is the forest and large areas of savanna like the Venezuelan llanos and the Gran Sabana harbor insignificant numbers of them. Savannas are plentifully populated with insects, particularly termites, and with small creatures such as snakes, lizards and mice, but the only large animal whose home is the savanna is the ant-eater which preys upon the termites. Even the deer of South America is a forest creature.

Since the arrival of Europeans, cattle have been introduced and have become more or less wild in some places, while cattle ranching is now carried on in most of the savanna areas. This activity has, however, to face certain obstacles which limit the number of stock on the range to a very low figure. In British Guiana, for example, it is not possible to run successfully more than one head to every 35 acres of savanna. Reasons are given by Follett-Smith (1930), Martyn (1931) and Follett-Smith & Frampton (1935). The principal factors are that the predominant grasses are coarse and unpalatable, and are deficient in essential minerals, notably phosphorus. Whether or not this is the cause for the absence of large numbers of wild grazing animals from the savannas, it is impossible to say. It is a curious fact that fossil evidence shows the existence of such a population during Pleistocene time. Today, the only true savanna fauna consists of the termites and the ant eaters predatory upon them. It will be seen, therefore, that since the arrival of the European, grazing has become a factor in the savanna habitat to a limited extent, but under primitive conditions it was entirely absent.

Large mounds erected by termites are a constant feature of the savannas upon the ancient highlands of Guiana and South Brazil. They are absent from the savannas of quaternary alluvial plains. Similar mounds present on the lowland alluvial savannas of British Guiana were attributed by Myers (1936) to termites (Syntermes) but by Martyn (1931) to parasol ants (*Atta*). The latter is probably correct. On the Guiana plateau, probably two species of termite are concerned, the one erecting low, flat mounds up to 3 ft. high generally and 6 ft. in diameter, the other building tall, irregular piles up to 12 ft. in height. The latter occurs on rising ground with the "clay with ironstone" type of soil, the former on flatter areas with the same soil or the "clay flat" type. Both kinds avoid inundated areas. Martyn (1931) found a special vegetation similar to that of the narrow savanna-forest transition to grow on the Atta mounds of lowland British Guiana, but on the Guiana plateau there does not appear to be a special vegetation on the termite mounds. The low type seen by the writer were covered with the usual savanna grass and the tall type are said to be bare of vegetation. Terrestrial termite mounds are only found in savannas, never in forests.

It may be conjectured that the termites find the ferruginous clay of the savanna soil a suitable material in which to nest, since it will solidify to some extent on being excavated and exposed to the air and is also so impermeable that the underground chambers and fungus gardens are kept from becoming flooded.

The influence of man and fire upon savannas is a very disputable matter. Many students have come to the conclusion that all or most savannas have been derived from forest as a result of constant fires set by man. Since the arrival of man in the Americas must be set between 10,000 and 25,000 years ago, this must all have come about comparatively recently and the process would presumably be still going on. It is true that all the major savannas are swept, nowadays, by regular fires, if not annually, at least every 2 or 3 years, the fires being set to improve the pasturage for cattle, to drive out game, or simply to keep the country open. Setting fire to grass has become traditional with Amerindians and they have evidently practiced it from time immemorial. Fire will take readily at any time in the dry season, and during short dry spells in the wet season, since sun and wind very rapidly dry out the savanna if there is an accumulation of old, dead grass. The occurrence of a regular climatic dry season is not a necessity for burning. Bunch grass savanna vegetation, as we know it, is strongly fire-resistant, the trees having a thick, corky, fire-proof bark and the herbs and shrubs underground perennating organs, which are not designed for water-storage, but, apparently, solely for regeneration after fire. Many such plants are highly specialized. An examination of the vegetation supports the view that it is a fire-climax.

On the other hand, fire does not occur readily in the forests, under the prevailing rainfall regimes in South America. It will be found that the boundaries of savanna and forest are almost invariably sharp, indicating that fire runs up to the forest border and stops there. Only in years of exceptional drought will it transgress. Where there are moist evergreen forests in tropical America the dry seasons are rarely long or severe enough to permit a destructive fire to take place. When this does happen, it will be years before a second burn is possible as in the meantime the bush recovers rapidly. In deciduous forests there is so little herbaceous ground vegetation that only a light ground fire can run through, which is seldom severe enough to harm the larger trees. It is not easy to destroy forest by this means, under South American conditions, unless soil conditions are adverse to forest growth and impede its vigorous regeneration.

Doubt may therefore well be expressed as to whether the sparse aboriginal population could have been capable of so much intensive destruction in the time available as to convert into savanna by means of fire without also grazing the vast areas we now see under grass. The Orinoco llanos alone cover about 100,000 sq. mi. It seems fairly well established that

fire can arise from natural causes in savannas, but it would scarcely do so in forest. Thus the retrogression to savanna could only have started after man's arrival. Secondly, if burning were the sole cause for savannas we should expect to find huge intermediate belts of burned and degraded bush in process of retrogression. In fact, such areas are limited. Fire could never be responsible for the alternation, seen in many places, of small patches of savanna and undamaged forest. In such localities fires are very rare and when they occur seldom penetrate the forests. The Aripo savannas in Trinidad have never been known to burn, nor are they grazed, yet never change. The shrubby elements in such sedge savannas are not even fire resistant. Bews (1939) stated that the tropical bunch-grass savanna does not depend upon fire for its maintenance and the writer is of like opinion.

The problem resolves itself into this: which came first, the fire or the savanna? Does the savanna burn frequently because it is a grassland, or is it a grassland because it frequently burns? The vegetation is, certainly, adapted to withstand fire, but it is equally well adapted to the adverse edaphic conditions of certain types of badly drained site. It has been shown that there are edaphic conditions typical of savanna and distinct from those of forest, and such habitats must have existed far back into history, long before man appeared upon the scene. If the savanna as we now see it is a fire-climax, we might expect to find some unmolested corner where some other original vegetation of the ill-drained site has persisted, but the writer knows of no such case. In the writer's opinion, the association of savanna vegetation and certain types of site is so strongly marked as to warrant the belief that grassland is and has always been the natural vegetation of such sites. Large stretches of grass, once developed, would become liable to catch fire occasionally from natural causes and burning would become more frequent after man's arrival. The vegetation would thus become secondarily adapted to withstand fire, but fire would not be a necessity to its maintenance, this depending upon drainage conditions. Intensive burning by man coupled with the fellings of the shifting cultivator, in later years and especially since the arrival of Europeans, has undoubtedly forced the forests back in some places and extended the savannas. It can, however, be argued that successful extension of the savanna has only taken place on habitats already marginal for tree growth.

It has already been observed that on the Gran Sabana, in parts of the Venezuelan mountains and of Trinidad, grassland has replaced forest in recent years as a result of fire, the grassland so produced differing scarcely if at all from the ordinary bunch grass savanna. When these areas are considered in detail in the next section it will be shown that the soil conditions were a predisposing factor. In drier regions an African-looking type of tree savanna has replaced forest, which is here more susceptible to burn and has less recuperative power. The type of vegetation produced, however, has nothing in common with "natural" or primitive neo-tropical bunch grass savannas; it is a strongly atypical, foreign element and depends directly upon man and his cattle and goats for its maintenance.

The absence under primitive conditions of anything which resembles the high-grass savanna of Africa is presumably due both to the generally higher rainfall in the Americas and the much less intensive and less prolonged assault by man and animals upon the plant cover. Forests which do not burn readily and regenerate vigorously when damaged, a small aboriginal population and absence of grazing animals, are factors insuring that grasslands which depend upon fire for their maintenance are of relatively rare occurrence.

In summary:

(a) The savannas of America were devoid of grazing animals until the arrival of Europeans and even now cattle are few.

(b) Large terrestrial termitaria are a feature of the savannas on ancient highlands.

(c) Savannas may be swept by regular fires and the vegetation is so adapted as to be fire-resistant.

(d) The savannas do not however depend on fire for their maintenance and are an edaphic climax.

Ecological Relationships

In the preceding sections a theory of a typical savanna habitat was elaborated, which may be briefly expressed as follows:

Savanna is the natural vegetation of the highly mature soils of senile land-forms (or, in some cases, of very young soils on juvenile sites) which are subject to unfavorable drainage conditions and have intermittent perched watertables, with alternating periods of waterlogging (with stagnant water) and desiccation. Frequent fires occur but are not a necessity for the maintenance of the savanna, which is an edaphic climax.

In the writer's view, it is essentially the alternation of waterlogging and desiccation which is too severe for forest growth. A great many species of trees are well adapted to withstand long drought periods, as the deciduous forests and thorn woodlands testify, but such trees must have favorable moisture conditions, which implies good site drainage, during the rains when their vegetative period occurs. Similarly, the swamp forests show us that there are tree species adapted to growth in more or less permanently waterlogged soil, or on periodically inundated sites. In the latter case, however, one of two conditions must be fulfilled: either the inundation must be of very short duration so that unspecialized forest trees are enabled to grow there, or else the effective portion of the soil profile supporting plant growth must never become absolutely dry, thus enabling swamp species to persist. A true watertable must be present. It seems that there are two classes of trees adapted to severe habitats at low elevations in the tropics: those adapted to withstand desiccation

of the soil, which cannot tolerate flooding, and those adapted to flooding, which cannot tolerate disiccation. The impermeable subsoils of savanna lands create perched watertables which come and go with the rains. The layers of the soil which are above this obstruction and to which tree roots are confined are waterlogged in wet weather and dried out completely at other times, so that a constant alternation of the two extremes is set up. The only trees which seem able to tolerate such conditions are the few oddly gnarled species found in savannas, whereas the xeromorphic herbs, particularly the bunch grasses, seem to be well adapted to the site. Grasses seem to have the faculty of growing vigorously whenever conditions are favorable, and going into a resting phase when they are not. Grasses, also, appear readily able to grow successfully under waterlogged conditions and to root in badly aerated soil. The entire savanna flora is xeromorphic in life form because of the almost perpetual state of drought, alternately physical and physiological, which it is adapted to endure. It is a different order of xeromorphy from that exhibited by "dry" forests or woodlands and is again a different type of specialization from that of the swamp formations.

We still have insufficient data to be able to suggest a completely satisfactory explanation for the variations in type within the savanna itself. The three main divisions, sedge, tall and short bunch-grass savanna, have been shown to be related to the relative lengths of the dry and waterlogged seasons, which is mainly an expression of climate. Within the tall bunch-grass savanna the four subdivisions—open, orchard, palm, and pine—seem to be related to soil conditions. Pine savanna is limited to the Antilles and Central America and is probably only a floristic variant of orchard savanna to whose flora pines are added in the region where they occur. Entirely treeless open savanna seems limited to soils which are clayey at the surface ("clay flat" type) or consist of clay overlain by stones ("clay with ironstone"). Such sites are commonly either flat bottomlands or the summits of knolls and ridges. Orchard savanna appears to be typical of savanna soils that are sandy at the surface ("sand over pan" soils) the sand horizon providing a suitable rooting medium for the savanna trees. Palm savanna is again associated with clay topsoils, but the manner in which they differ from those of open savanna has not been worked out by the writer. In general, it would appear that palm savanna soils are wetter than those of open savanna, probably to the extent of having a deep source of underground water below the clay pan. It is probably fire that prevents these palms from forming up to dense groves.

The application of these general theories to particular cases will now be discussed in detail.

TRINIDAD

The savannas of Trinidad occur only as scattered tiny patches which used to be or still are surrounded by evergreen forest. They cannot, therefore, be of climatic origin. Marshall (1934) regarded the Aripo savannas as a type of swamp vegetation and attributed the others to the influence of fire. The St. Joseph savanna, certainly, has at least been profoundly modified by fire and grass now covers certain areas in the plains formerly under forest, but fire does not seem to be the correct explanation for the lowland savannas in general. Their occurrence as small patches in forest with sharp boundaries is against it, also the presence of endemic plants and the development in the centre of the Piarco savanna of the special type of sedge savanna with *Byrsonima verbascifolia*. Besides, the savannas are so obviously associated with peculiar conditions of soil and site involving adverse drainage. All the savannas of the plains occur on terraces, that is, on remnants of an ancient landsurface. Beard (1946) traced the geological history of Trinidad during Tertiary times, leading to the evolution of the present topography. During most of the Tertiary period the Northern Range existed as land but there were shallow-sea conditions to the south of it, with perhaps occasional islands formed by what are now the hill ranges of the centre and south. During Pleistocene times a great alluvial plain was built up, coextensive with and similar to the present llanos in Venezuela north of the Orinoco. As this plain matured and a senile topography developed with special soil types, savannas would gradually have occupied its surface and the forests have shrunk to the stream vegas and the hills. In more recent times earth-movement led to the formation of the island of Trinidad which became slightly raised while the Gulf of Paria was depressed and inundated. A new erosion cycle was initiated on the island, the rivers were rejuvenated and dissected the great plain little by little. As its surface was removed, an undulating topography was substituted for flat and drainage conditions again became good, so that forests could reoccupy the land. Only a few small isolated remnants of the ancient landsurface still exist and have remained covered with savanna. This explains the patchy occurrence of the Trinidad savannas. They are the vanishing survivors of a bygone age, the dwindling relics of a past geological period.

The diagrams in Figure 30 show in profile the association of soil, vegetation and landform at the Erin, Piarco and Aripo savannas. The Erin savannas are small plateaus along the summit of a watershed, flat expanses with the typical savanna soil types, sand over clay or clay with ironstone. At the margins of the plateaus or slightly below them, an abrupt transition to forest occurs, the forest occupying highly dissected topography with soils of favorable drainage. The savannas evidently occupy remnants of an earlier extensive plateau which is being eroded away, and the forests will be very gradually closing in. That the grass still persists in some cases on the upper part of the erosion-slope bordering the plateau is probably due to fire.

The Piarco, Mausica and O'Meara savannas are also on similar plateau sites with similar soils but

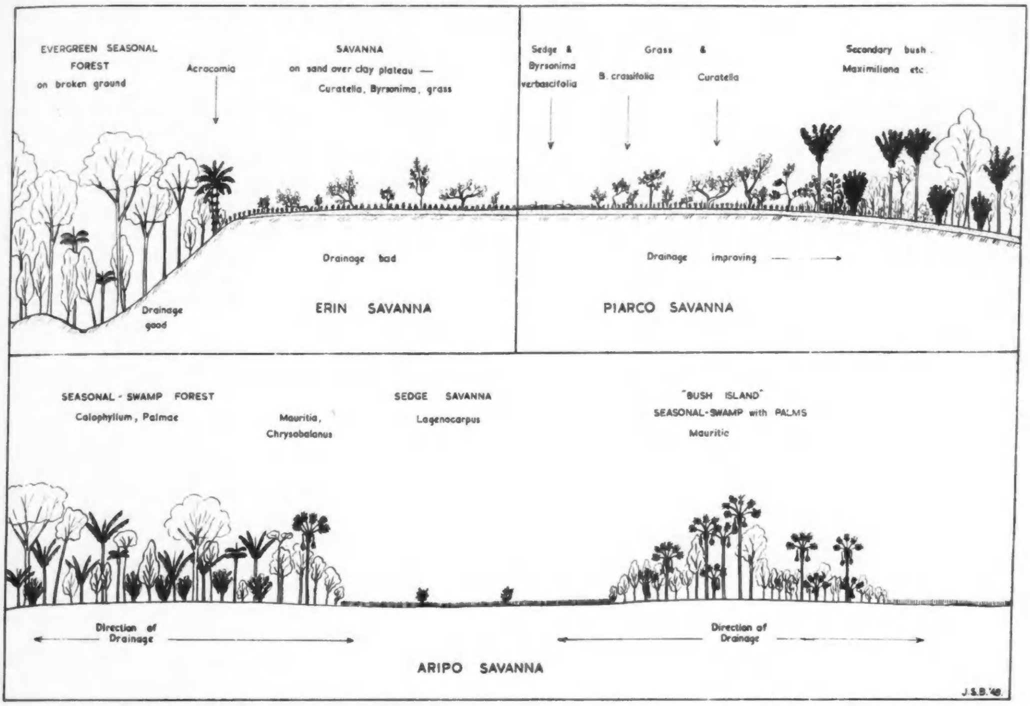

FIG. 30. Sketches of vegetation and site profiles for the various savannas in Trinidad.

there is not the sharp drop to dissected country at the edges, the plateaus sloping down gradually to the rivers. In the circumstances there are no substantial physical differences here between savanna and forest soils, and no abrupt transition to forest is to be seen. It may have existed formerly but has been obscured by burning of the forest. There is, however, a difference in drainage between savanna and forest sites. Subsoil drainage being impeded, virtually all drainage must travel across the surface. The savannas are situated in the centre of the terrace-plateaus where drainage is at its worst and where most waterlogging occurs. This is particularly clear at the heart of the Piarco savanna where there is even a special and reduced plant community, with sedge and *Byrsonima verbascifolia,* clearly associated with drainage conditions. Forest growth occupies the outer parts of the terraces where the land is sloping slightly towards the rivers. The rainfall here is substantially the same as at the Erin savanna and is not very high, about 60 inches annually, so that waterlogging even of soils with claypan only becomes severe where the ground is very flat. There is nowhere any sharp change in site conditions here such as occurs round the Erin savanna where the ground falls suddenly away from the savanna plateau and since man began intensive burning there is no doubt that these savannas have expanded onto marginal sites.

Other grasslands described by the writer as "cocorite savannas" occur on the northern plain and are known to have replaced forest in recent years as a result of repeated fires. They occur only on flat terrace sites where drainage is somewhat impeded and where habitat conditions are already close to those of the savanna.

It is interesting to observe that in other parts of Trinidad where burning is equally intense, at the western end of the Northern Range for example, the land has not gone to grass in the same way. It is true that "savannas" of the bracken fern *Pteridium aquilinum* (L.) Kuhn have appeared and that after a burn, grass may cover the ground for a short while. Grassland has only become established on these mountains where erosion has removed the soil, e.g. the St. Joseph savanna. There are no instances on hilly lands in the lowlands where burning has by itself established grassland. Fire-grasslands have only appeared in this island on flat, ill-drained lands where conditions were already not far removed from those of existing savannas.

It has been noted in the description of the Piarco, O'Meara and Mausica savannas that these can be seen to have expanded of recent years as a result of fire. The expansion areas show a combination of the true savanna flora with that of the cocorite grasslands described above. It may well be that in the course of time if burning is continued the true sa-

vanna flora may colonize all of the cocorite grasslands. Already, fringing the Piarco group of savannas, fire has brought in grassland where forest was before. Given protection from fire, forest would return unless some permanent alteration in the soil had taken place in the meantime. In these lowlands there is no evidence of this. In all cases in Trinidad where savanna has extended it has done so onto lands where soil and drainage conditions were already marginal for forest and where the incidence of a new factor, fire, hostile to forest, was able to tip the balance in favor of the grassland.

The Aripo savannas are of the sedge type and differ from the other savannas of Trinidad owing to the high rainfall which makes waterlogging more prolonged and shortens the drought period. This may be a convenient point at which to inquire how the habitat of sedge savanna differs from that of the bunch-grass. Sedge savanna is clearly, in a general way, more hygrophilous than the bunch-grass, but not in the sense in which Bews considers the high-grass savanna as more hygrophilous. It might be preferable to describe the sedge savanna as more hydromorphic, for it embodies many of the characters of swamp. As the dominant plants are still more or less xeromorphic, however, and as the site conditions are still closely similar to those of bunch-grass savanna, it must rank as a savanna and not as a swamp community. It is a type of savanna which shows affinity to swamp formations. Sedge savanna is found where inundation is prolonged and desiccation of short duration. It occurs in areas of very high rainfall or in depressions where water collects in the rainy season.

The soil beneath the Aripo savannas is exactly the same as that under the adjoining forest, nothing but surface drainage conditions differentiating the two communities. It has been shown that some of the patches of savanna occupy very slight depressions in the flat alluvial terrace, possibly sites of the occluded bends of some meandering river of the late Pleistocene. Other patches are dead-level stretches on the terrace. These sites, since the subsoil is impermeable, fill with water and can support only an herbaceous vegetation. In the forest areas surface drainage meandering through the hogwallow channels is sufficiently good to permit of tree growth, as is the case in the vicinity of the Piarco and related savannas. At Aripo both savanna and forests are different from those further west owing to the higher rainfall, and a series of highly specialized forest types are present intermediate between the savanna and the normal evergreen seasonal forest. It would appear that the high rainfall here permits the establishment of specialized forests on sites which under drier conditions would carry only savanna, and the savanna is restricted to relatively small patches which alternate in a kind of mosaic with the woody communities. This phenomenon is reported elsewhere, from French Guiana for example, where sedge savanna occurs in forest. It forms an interesting parallel to the tendency of short bunch-grass savanna to occur in a mosaic arrangement with bush and forest under very dry conditions, at the other end of the scale, so to speak.

The St. Joseph savanna consists of two separate communities, the Curatella-Byrsonima type and the Myrcia-Roupala type. The writer suggests that the latter is the primitive form of this mountain savanna and that intensive burning due to man's interference within the last two centuries has converted former areas of Myrcia-Roupala savanna and of forest (where intense erosion has followed) into a more fire-resistant type of grassland. The herbaceous growth has not greatly changed but *Myrcia stenocarpa* and other shrubs which have a low resistance to fire have given way to the fire-resistant Byrsonima and Curatella. The Myrcia-Roupala areas today occupy sites which are not so readily exposed to fire and appear to be but seldom burnt whereas the Byrsonima-Curatella areas are thoroughly burnt over almost every year. The latter are conspicuous from the plains whereas the former are not and blend into the surrounding high woods.

In both cases the occurrence of savanna may be attributed to the virtual absence of soil. Such little soil as there is on the surface (and in crannies to afford a meagre root-room) lies in contact with an impermeable, impenetrable "pan" of bedrock and the same effect of alternating waterlogging and desiccation remarked in the lowland claypan soils is present here also. Since man burned off the vegetation and exposed the soil, erosion has certainly bared the bedrock and expanded the savanna. Occurrence of a primitive savanna in prehistoric times must be explained from the exceptionally hard and quartzitic nature of the rock in this locality. Formation of soil on a mountain side can only occur if weathering proceeds at least as fast as erosion removes the surface. Where the rock is very resistant to weathering, soil formation may be indefinitely postponed.

THE ORINOCO LLANOS

The eastern part of the llanos, particularly the various extensive mesas which are not flooded in wet weather, is an area such as inspired the ideas of Schimper and others about the climatic origins of savanna. The rainfall is low for American savannas, averaging only 40-45 in. a year, and the vegetation gives the impression of even greater dryness. Schimper considered the climate "hostile to woodland" because of a long rainless dry season of five months and a continuously rainy wet season, but now that we have meteorological records we know that this characterization of the climate is not the correct one. Similar climate elsewhere can and does support deciduous forest.

Conditions on these llanos are only a magnification to very much greater scale of those in the Trinidad savannas, for we have here, still intact, the great plains of which they formerly were a part. The savannas both of Trinidad and the Orinoco llanos occupy flat alluvial terraces of Pleistocene age which are little dissected and feature soils with impeded

subsoil drainage. The nature of the soil on the llanos appears to be essentially the same as the predominant type on the lowland savannas of Trinidad, in that it is a sand over clay, and the land form is essentially similar. Diagram A in Figure 31 shows a profile arrangement for the Mesa de Guanipa. Most of the area consists of high terraces which undulate very gently and are broken by occasional knolls capped with ironstone. The rivers meander in flat valleys cut down below the high terraces, the valley floors being covered with savanna except immediately along the stream, where Mauritia groves occur.

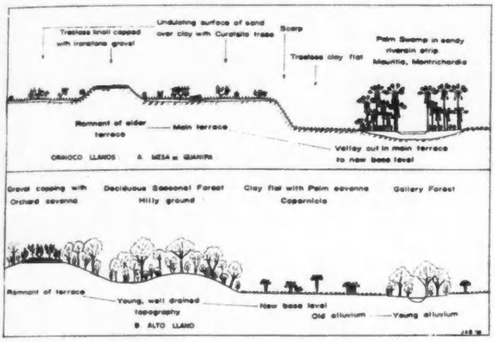

FIG. 31. Sketches to show the association of vegetation and site on parts of the Orinoco llanos.

The ironstone knolls are a feature not present in Trinidad and seem to be relics of a surface on which ironpan soils were well developed. Such soils have not been reported in situ in the area today and evidently represent a phase in the early history of the landscape. These knolls are probably very persistent as the stone capping must be a protection against erosion. On the high terraces generally, the upper sandy horizon of the soil is rather looser than in Trinidad and according to Pittier is subject to windblowing. This might account for the absence of hogwallow structure and for the lighter color which implies lack of organic remains. The low rainfall probably accounts for the preponderance and fine growth of Curatella, which flourishes under drier conditions than Byrsonima. Pittier observed that the savanna trees prefer high ground, except for the stone capped knolls, and avoid the river flats, accounting for this on the ground that a high water table in such depressions would be an obstacle to the proper development of a tree's root system. The present writer's observations of the root system of these species show that it is markedly superficial, not deep such as Pittier supposed, but it is sensitive to lack of aeration. The more prolonged waterlogging of the low flood plains would certainly discourage growth of these trees.

The Mauritia groves bordering the rivers are a swamp type of vegetation and are evidently associated with perennially swampy conditions. In the rainy season the *morichales* are inundated and in the dry season the soil is still wet. Water relations differ from those of the savanna where there is an intermittently high perched water table in the rainy season, and no water table at all during the dry period.

The distribution of vegetation on the *alto llano* is shown in B of Figure 31. This area to the north of the llanos proper is somewhat dissected and the high terraces represented on the Mesa de Guanipa have here been cut up into undulating country with the old surface persisting here and there on a ridge top capped with ironstone gravel. This again parallels conditions in Trinidad, and as in Trinidad the undulating country is forest covered, here by a deciduous forest owing to the lower rainfall, with patches of savanna on the residual surfaces. Savanna trees occur on the ironstone gravels here although they do not on the llanos proper. The greater dissection of this area has greatly extended the river flood plains, relatively narrow on the Mesa, here broad expanses covered with palm savanna. A new peneplain is being formed at a lower level than the old and its clayey topsoil encourages the palm type of savanna.

THE VENEZUELAN CORDILLERA

In these mountains the bunch-grass savanna has taken possession of slopes which have been cleared, cultivated, eroded, abandoned and subjected to frequent fires. The change has occurred within the period of European settlement, that is, the last 400 years. It would appear that the savanna has been enabled to establish itself in this way not solely owing to the fires but owing also to the severe erosion of the mountain slopes. Present vegetation has but little between it and the bedrock. The situation is comparable to the St. Joseph savanna in Trinidad and is another example of the establishment of savanna through burning on a marginal site. Fire alone would not degrade the forest to grass, and secondary bush of some kind would always spring up. A secondary factor in the form of adverse soil conditions of the type favoring savanna must always be present to enable bunch-grass savanna to supersede a forest community.

THE LESSER ANTILLES

Similar remarks apply to the Grand Savanna of Dominica where the soil suffers from impeded drainage and the natural conditions are in many ways not unlike those typical of savanna lands. Most of the "savanna" however is rather clearly just burnt-out bush. None of the typical elements of American savannas, save only *Sporobolus indicus*, are present here and in the writer's opinion the area was formerly all forested.

Grasslands in Antigua are pastures with thorn bush, created by man, and merit no discussion. The small savannas of Barbuda, on the other hand, appear to be natural. The whole island is formed of flat limestone terraces bearing very little soil and

as a result carries only a low evergreen bush which is to be regarded as rock-pavement vegetation. The savannas occupy slight depressions where water collects after rain. The soil is a reddish clay overlying limestone sheet rock and is thus of the "clay flat" type. The savanna alternates rapidly with the bushland according to very slight variations in level and soil-depth, forming a mosaic of grass and bush types reminiscent of the Chaco parkland and certain very dry areas in Cuba. Such a mosaic arrangement seems to be typical of areas of low rainfall where the waterlogging factor is at a minimum. The writer found the grass here to be about 18 in. high at the end of the rainy season and it may perhaps be regarded as a short bunch-grass savanna.

HISPANIOLA

The open savanna on the central plain of Haiti is a typical example of the association of savanna with an old peneplain, where the soil has developed impedance to drainage. The hardpan in this case is of a calcareous nature and lies somewhat deeper than is usually the case in these savanna soils, but the effect of the seasonal perched water table is there none the less. The silty-clay topsoil is no doubt responsible for the treelessness of this savanna. Both topsoil and pan reflect the influence of the parent limestone on the soil morphology. Other rock-types on the same site would have resulted in a "sand over pan" soil, with the pan formed of ironstone, instead of this, which should be referred to as the "clay flat" type.

The ecological relationships of the orchard savanna are more difficult to assess, since data are insufficient. Dr. Curtis believed the orchard savanna, in the area studied by him, to be due to fire and this may well be the case. If so, it will be another example of the ability of savanna to advance and colonize marginal sites when the forest cover is destroyed by frequent fires. On the other hand, the orchard savanna may equally well be natural. It occupies sites marginal to those of open savanna though not to such an extent as to permit the growth of forest. The latter is seen only along the bottomlands where the soil will be a deep, young and well drained alluvium. Dr. Curtis' "knob-hill country" is in a more advanced geomorphological phase and the rising ground in this case should have been rejuvenated to the extent of being able to support forest of some kind. The soil of the intervening bottomlands has now matured, presumably, and developed a profile like that of the savanna plateau, so that the vegetation has retired to savanna. On the knob-hills we should rather expect to find closed forest or bush but instead we find open pine savanna, where the grass is said to be ecologically dominant. None of the trees listed, besides Pinus, occur normally in savannas and this is probably a fire climax. A community where pine is present is not necessarily pine savanna, the tree being a component of several very different formations. As has been shown, the principal role of Pinus in Haiti is to form pine forests in the high mountains which are thought to have followed destruction of mixed montane forests by fire. These pine forests are grassed beneath, but the pine and not the grass is dominant. Pine savanna is only found here and there in the lowlands where the pine has added itself to pre-existing savanna communities.

The Themeda savanna of the central plain is not in every way typical of tropical savannas, perhaps due to its situation at an altitude of 1700 ft. and near the borders of the tropical zone, which may render the climate of a subtropical character. The genus *Themeda* is not recorded elsewhere for neotropical savannas and is said to be a sod-forming grass rather than a bunch grass. The soil has the typical drainage relationships of savanna soils but differs in structural characters from the usual pattern. There appears to be some resemblance here to the South African "High Veld," a treeless grassland of high plains with *Themeda triandra* dominant and growing upon what van der Merwe (1941) described as gley-like podsolic soils.

The "dry savanna" of Haiti should probably be classed as short bunch grass. The dominant grass, Uniola, reaches a height of 36 in. when in fruit but the general height of the leaves is much less and the growth is very open with wide spaces between the tussocks. Soil throughout is virtually absent, the surface being formed of a mass of small limestone fragments. While this savanna could have been of fire origin in pre-Columbian times, there are factors which make this doubtful—its great uniformity, the localization of *Tetramicra ekmani* which is not found elsewhere, and the evident symbiotic relations of the latter with Uniola, implying a long-term association. We have here one of the rock-pavement types of savanna.

CUBA

Cuba was the country where the association of savannas with a special type of soil and site was first suggested and worked out in detail (Bennett & Allison 1928) and it is therefore unnecessary further to labor this point, save for a few supplementary notes. The savannas occur predominantly on flat or gently undulating land, and where they do not, impervious rock will be found close to the surface. Predominantly, the soils have intermittent perched water tables due to impermeable subsoils. Only two of the savanna soil types depart from this pattern, the Nipe clay and the Norfolk fine sand. The former is a very peculiar soil derived from serpentine, highly weathered and regarded as a true laterite by Marbut (1932). It is very probable that impeded drainage is actually present. The Norfolk fine sand is a very deep soil without any impervious horizon: it occurs on areas of low relief with a high water table in the rainy season, when the savannas are probably flooded. If the dry season is so severe that the loose sand dries out very deeply and the water table vanishes, this would create the conditions necessary for savanna.

In some of the dry parts of Cuba, there is an

alternation of savanna with thorn and cactus bush forming a mosaic, rather as on Barbuda. It would appear that under low rainfall conditions patches of xerophilous bush are enabled to occupy small areas of very slightly higher relief which in a wetter district would be part of the savanna. The savanna habitat has to feature an alternation of waterlogging and desiccation, and where rainfall is low the latter will predominate, severe waterlogging only occurring on low spots. Raised patches would tend to be free from waterlogging and would resemble ordinary well-drained soils of the vicinity, carrying the climatic vegetation. A parallel phenomenon at the opposite extreme has already been suggested for very high rainfall areas, when discussing the Aripo savannas of Trinidad. Where rainfall is high and the dry season mild, waterlogging of the impeded soils will predominate for most of the year and a specialized, swamp-like forest may occupy sites which under a drier climate would carry savanna.

Marie-Victorin & Léon commented on the physiognomic resemblance between artificial grasslands with trees on which cattle ranching is practiced in Cuba and "African savannas of the natural *Acacia-Andropogon* type"—that is, the High-Grass Savanna of Bews (1929) or the High-Grass Low-Tree Savanna of Shantz (1923). These Cuban savannas should evidently be regarded as the equivalent of the African high-grass savanna and are an indication of the artificial nature of the latter.

CENTRAL AMERICA

Charter's work on the ecological relationships of forest and savanna in British Honduras (1941) is monumental and the writer is glad to acknowledge that it provided the incentive for this wider study. His theory of the aging of the soil and site on alluvial plains is a hypothesis which we may see fit to accept or not; to the writer it is convincing. The facts about the savannas and their habitats may be summarized as follows. A generalized profile diagram appears in Figure 16.

Several types of savanna are present: sedge with palms, bunch-grass with pine, or "orchard." There can be no possibility of a climatic explanation for them, situated as they are in a moist region surrounded by forests. Their occurrence is patchy and fire is clearly only a subsidiary factor. All the types of savanna are associated with impeded drainage soils. Variations in drainage differentiate them from one another and from forest types. Very much as at the Aripo savannas in Trinidad, the savannas are associated with several forest types, all differentiated by drainage factors and disposed in a mosaic arrangement about areas of pessimum drainage.

Conditions in British Honduras are repeated in Guatemala and Yucatan. Pine savannas occur in the interior of the Honduras Republic on hilly ground. We know little about them and have to presume they are equivalent to the "mountain pine ridge" of British Honduras. Of savanna lands elsewhere in Central America we know nothing significant other than that they occur on coastal plains and are of the usual bunch-grass formation with *Curatella americana*.

VENEZUELAN GUIANA

In this gently undulating region based upon ancient rocks, with soils of the sand over clay or clay with ironstone types, the savannas are clearly associated with adverse soil drainage conditions due to the gentle slopes and impermeable subsoils. Across the area from Ciudad Bolívar in the north-west to Tumeremo in the south-east, the rainfall gradually increases from 40 to 60 in. a year, but the savanna does not change. On the other hand, the forests which occupy the mountains and depressions show a marked response to the change in climate, grading from evergreen or semi-evergreen forest in the south-east down to deciduous forest and thorn bush. These forest types are climatic formations, growing on favorable soils. Mountains and hills are forest covered wherever there is adequate depth of soil, owing to the sloping, well drained land and young, immature soil profile, and even carry poor forest where there is naked rock if it has deep crevices to root in. Shallow impervious rock favors savanna, as is sometimes seen on the mountain slopes. Forests of depressions and river flats are essentially "gallery forests" and are found on deep, pervious young alluvia.

Diagrams A and B of Figure 32 show the arrangement in profile of site and vegetation, A being typical of the north-western part near Ciudad Bolívar, and B of the area near Tumeremo. Conditions at A are very like those on the Venezuelan llanos, the same gently undulating ground with light, pale, sandy topsoil and heavy red clay subsoil, and occasional knolls capped with ironstone. A new feature here is the granitic outcrop clad with thin deciduous forest, and the streams are bordered with this same formation instead of by dense *morichales*. The Mauritia palm is only present as odd specimens along the stream banks. Deciduous seasonal forest is replaced along the depressions and drainage channels by thorny thickets in some places, for which the explanation probably is that soil conditions are intermediate between those of the savanna and the riverain forest;

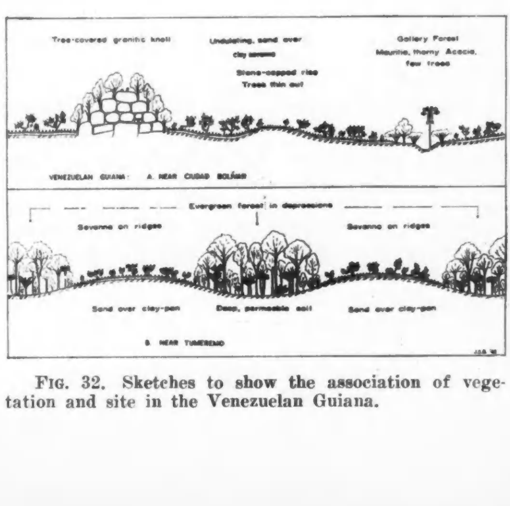

FIG. 32. Sketches to show the association of vegetation and site in the Venezuelan Guiana.

alluvial soil present but probably to no great thickness.

Diagram B shows the alternation of low, rounded hillocks covered with savanna and shallow depressions filled with evergreen forest which is characteristic of the region around Tumeremo. In plan, the savannas are seen to be more or less round patches set very regularly in the forest like a huge checkerboard. The perpetual alternation of hillock and depression is like a hogwallow surface enormously magnified. There are sand over clay soils on the hillocks under the savanna and deep brown loamy alluvia under the forest. This appears to be a senescent landscape. Mature soils with impeded drainage have developed already on the tops of the rises, the first place where they would do so. Alluvium is still being gradually deposited in the depressions which in time will be levelled up with the hillocks into a more or less even plain, by which time savanna will have developed on the flats also. The hillocks eventually will come to form, in all probability, ironstone-capped knolls in an extensive savanna. We have here savanna country in the making.

Llewellyn Williams' travels further to the westward in the Venezuelan Guiana show us sometimes undulating savannas like those seen by the writer and sometimes low-lying flood-plains of the lower river courses where conditions are like those of the llanos north of the Orinoco. There is always a general division of the landscape into savanna plains and forested mountains, an arrangement broken only by the *rebalse* swamp forests on the flood plain of the lower Caura, which correspond to the *varzeas* of the Amazon. All Williams' savannas are of the sedge or bunch-grass types and occupy typical soils—sand over marl, sand over compacted quartz gravel, and so on.

BRITISH GUIANA

The so-called "wet savannahs" of British Guiana are incorrectly termed, according to our definition, and should be regarded as herbaceous swamps. There are true bunch-grass savannas in the east near the Berbice River. Follett-Smith's description (1930) of two soil types in these savannas show both of them to be deep sands, apparently without the impervious subsoil which we are accustomed to expect. The most widespread of the two soils, the "brown sand" type, changes from a fine brown sandy topsoil at a depth of two feet to a slightly heavier red-brown loam, and it seems unlikely, from the description, that drainage impedance can be very severe. Nothing is said by Follett-Smith, however, about such things as drainage and water-tables and so we are left guessing. Conditions may be similar to those inferred for the Norfolk fine sand of Cuba, that is to say, a high water table in the rainy season which vanishes altogether in the dry. This is unlikely owing to the high rainfall of this area, but due to the latter and the flat ground, there may be effective drainage impedance in spite of the small amount of textural variation in the profile, percolation being unable to dispose of rainwater quickly enough. One way or another, the behavior of the shallow "pans" which are lakes in the wet season, parched in the dry, indicates an intermittent water table.

A very interesting point is the growth of bush upon the ant mounds in the savanna, which is "capable of withstanding the periodic savannah fires and resembles that found in the narrow transition zone between forest and open savannah country" (Follett-Smith). This seems to prove, for one thing, that it is the soil and not fires which is responsible for the maintenance of savanna, and secondly that adverse drainage is present in this savanna, the raised ground of the antheaps providing a site clear of waterlogging on which bush can develop. That the antheap vegetation resembles that of the forest margin is also significant since this is a zone where drainage begins to be improved.

Raised reefs of coarse white sand are covered not with savanna but with a low evergreen scrub called *muri bush*. It would be very interesting to have more data on the ecological relationships of this community. Evidently the raised land-surface confers immunity from waterlogging, but one may suspect, from the fact that these sand reefs have at their margins springs or waterholes, that there is an impermeable layer somewhere fairly deep in the soil profile. In some way, at least, soil drainage conditions must be superior to those of savanna but inferior to those of forest.

DUTCH GUIANA (SURINAM)

Climatic and soil conditions in the Surinam savannas are similar to those in British Guiana. From the rainfall figures one would expect normally to find rain forests in this region and they are in fact present surrounding the relatively small savanna patches. There can be no question here of climatic savanna. Both sedge and bunch-grass types are present, called by Lanjouw (1936) "wet" and "dry" savannas respectively, which is eloquent of their relative habitat. The flora of the sedge savannas is very closely similar to that of the Aripo savanna in Trinidad, so that similar soil conditions may be inferred. Both Lanjouw and Ijzerman (1931) appeared to regard the soil as readily permeable, but the writer doubts very much if this is really so. From their descriptions, the savannas are under water or waterlogged in the rainy season. Perhaps the flat sites and heavy rainfall are between them too much for the soil porosity. It does not seem to have struck the Dutch investigators as significant that the savannas occur on flat plateaus forming the watersheds between the rivers, which are either portions of an ancient peneplain like those of Trinidad or the most mature parts of an alluvial plain in formation, as in British Honduras.

Drainage is bad because of the flat and undissected landscape and we might expect that the special savanna soils would have developed. If the soil is very sandy to start with, however, no very marked differentiation into textual horizons would occur.

We have here the usual association of savannas with a senile landscape and defective drainage, and the writer does not believe in the theory of the Dutch that leaching of the soil is responsible for savanna formation.

Here and there in the Surinam forests there are found patches of low evergreen forest and scrub named locally *moeri-moeri bush* and described by Lanjouw as savanna-forest. These are considered by the Dutch to be areas of forest in process of regression to savanna as the soil becomes impoverished. The *moeri-moeri* appears to occur on two types of site: rock pavements and deep sandy soils. In the former instance, with sheets of granite rock beneath and very little soil, we are clearly not dealing with a degraded forest soil. Rather the opposite is true, for more soil can be expected to form on the rock in time, permitting a finer forest to develop. In the second site, details of the soil are less clear, but presumably the *moeri-moeri* is to be found on reefs of quartz sand like the *muri* of British Guiana. The two names taken from the aboriginal are evidently the same. Under these circumstances, the *muri* (or *moeri*) sand is certainly highly leached, but its drainage relationships differ from those of the savanna and drainage provides a more acceptable basis for an understanding of these communities.

FRENCH GUIANA

The savannas of French Guiana are only a continuation of those of Surinam and the same remarks apply to them. Both sedge and bunch-grass savanna are present, the latter corresponding to the general type for the Guianas and the former very closely to the Aripo savannas of Trinidad.

No soil data of any kind were given by Benoist (1924) who considered that the appearance of these savannas in an area where we should normally expect to find rain forests must be due "to the intervention of man." It was unfortunate that the man-made pasture lands he cited had a totally different flora from the true savannas, although they had been created by clearing, burning and grazing without the deliberate introduction of extraneous pasture grasses. Besides, how could this theory account for the frequent rapid alternations of small patches of forest and savanna across sharp boundaries? The similarity of the sedge savannas to those of Trinidad is so close that similar ecological relationships must be inferred and drainage taken to be the vital factor.

If Benoist's rainfall data are correct, it is interesting to note that the savannas here occur under the highest annual rainfall of any in the Americas—140 in.

THE GUIANA HIGHLANDS

At Santa Elena on the Gran Sabana, the annual rainfall is approximately 70 in., with a weak dry season of 3 months. The rainfall regime is the same as that of Trinidad and the same evergreen seasonal forests are found on the Gran Sabana on favorable soils. In the British Guiana interior the rainfall is less and the dry season more severe, but the savannas throughout are composed of the same dominant plants. Open savanna predominates on the Gran Sabana and orchard on the Rupununi, but the grasses are the same. Trees drop out on the Gran Sabana probably because of the clay topsoil. Unlike the Venezuelan llanos, there are seldom here any vast stretches of unbroken savanna.

A diversified landscape is the rule, savanna covering the flat ground and forest the hills and mountains with exceptions in both cases, so that some forests are found on flats and some savanna patches on mountains. This diversity of landscape is strongly against a climatic origin of the savanna, for unless the forests are on any particularly high mountain they must enjoy the same climate as the savannas. Jones (1930) sought a geological explanation, with the savanna lands on sandstones and the forests on igneous rocks, a theory that is based on soil fertility. It is not, however, in accord with the facts, as there is no such correlation of geology and vegetation here. Predominantly, there is a correlation of site and vegetation, which strikes one from all the accounts as well as on the spot. There are exceptions, but they can be satisfactorily explained. In general, as everywhere else in South America, savanna covers flat lands with impervious subsoils and forest occupies sloping or other well-drained land.

Follett-Smith & Frampton (1935) showed that in the Rupununi savannas of British Guiana there is little essential difference in chemical composition between savanna and forest soils. The savanna soils correspond, however, to the usual types in physical structure. On the Rupununi, sand over clay is predominant with many ironstone-capped knolls, as on the *mesas* of the Orinoco llanos. Both these types appear on the Gran Sabana, together with sand over ironpan, a silty soil over rock and "clay flat" soil, the last being the predominant type found by the writer between Santa Elena and Roraima. The flat bottoms of the valleys in this region were found to consist of a very compact clay soil bearing savanna, with termite mounds scattered on the drier places and Mauritia palms on the wetter. Gallery forest borders the watercourses. The high ground takes the form of a series of very flat plateaus bounded by scarps, the whole landscape being arranged as shown in Figure 33. The uplands are again mostly composed of clay flats, the soil here being even more compact and lighter colored at the surface than in the river flats, strewn with occasional stones and with few termite mounds. Ironstone-capped rounded knolls are frequent. Forest is sometimes found on the scarp faces and on other localized areas of broken or sloping ground on the Sabana where we might expect to find it owing to the improved drainage, but not invariably. The majority of such sites are covered with grass and forest is usually found nestling into deep valleys and folds of the ground. In many places, particularly on the boundary of the forest area to the north-east, the writer found clear

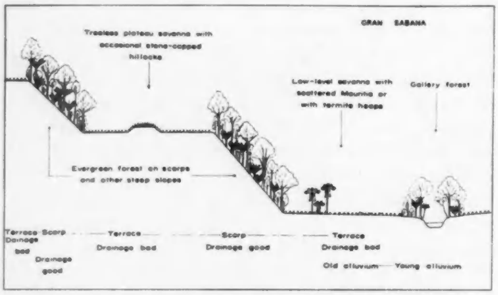

FIG. 33. Sketch to show the association of savanna and site as believed formerly to have existed on the Gran Sabana. The forests of the scarps have now mostly been destroyed by fire.

signs of regression of the forest due to fire. A fire theory, as proposed by Christoffel can, however, only be accepted with reservations.

The writer believes that the flat areas on the Gran Sabana are original grassland, associated with intermittent perched water tables, and that all the scarps, broken country and streambanks were covered with forest before man's arrival. The original pattern, in fact, would have been as shown in Figure 33. Since man began regular firing of the savanna the forests have been very gradually eaten away and now mainly nestle behind the protection of a topographical obstacle. It is surprising how often a grass fire will stop at a sharp ridge or declivity. One is compelled to believe in the natural occurrence of savanna on the flats, independently of fire, owing to the very typical senile landscape with its typical soils and also owing to the termite mounds which are unknown in forest.

The forests between Santa Elena and Roraima were observed by the writer, both gallery forests and those on the hills, to belong to a somewhat specialized type indicative of adverse soil conditions, so that their replacement by savanna after fire is only another example of the extension of savanna onto marginal sites under the influence of burning.

To the south of Santa Elena on rocks of the basement complex a very patchy alternation of forest and savanna is seen on both hill and flat. The forest is no longer a specialized type, and there is no clear evidence of recession due to fire. Forest and savanna soils were clearly quite different, the forest soil a deep and permeable clay, stoneless, dark brown at the surface, the savanna soil a bright red clay thickly strewn with ironstone. The writer was unable to study these soils and the question must be left open for the present.

Near Santa Elena to the North there are some uplands of deep white sand overlying rock which carry a low and very open scrub, evidently "muri bush." South of the Rupununi, the type of muri on granite rock pavement appears, in a very patchy landscape of forest, muri and savanna. Soil depth and drainage are evidently the controlling factors.

THE AMAZON BASIN

The majority of savannas on *terra firme* in the Amazon basin are located in the drier region of the lower course, but there are some in the high rainfall region of the Atlantic littoral and in the delta. Even if they were confined to the drier region, it would not be readily possible to ascribe their cause to the climate since they are but small patches set in predominantly forested country. The forest of the area does reflect the climatic regime. It is not rain forest but seasonal, relatively short and with many deciduous species. Bouillenne's theory of the climatic origins of the savannas is a marvel of plausible ingenuity, but scarcely credible. Had he also visited the Atlantic littoral, one wonders how he would have explained the savannas in that entirely flat and featureless region. It will be recollected that Bouillenne discounted the influence of the soil on the grounds that (a) the bulk of the Amazonian forests are on sand, and (b) the same sandy and stony soil carries both forest and savanna. The first observation is true, but to say that since savannas as well as forest are on sand, it is the same soil in both cases, is a *non-sequitur*. It matters not the surface soil is sandy; what is important is what happens underneath. Sandy soils of forests are deep and well drained with adequate root-room. Sandy soils of savannas are shallow and obstructed by clay or iron pan.

In support of this contention we cite Marbut (1932): "throughout the Amazon valley the soil consists of (1) topsoil, (2) iron oxide layer, porous and slag-like, (3) mottled layer, (4) grey layer, (5) unconsolidated clay and sand. The mottled zone, with or without the induration of its upper part to an iron oxide crust, is found invariably beneath the surfaces of broad plains with flat or nearly flat surfaces or where the relief shows that dissection is very recent. It is not found on mountain slopes or in thoroughly dissected regions where the dissection is old."

This gives us the key to the whole problem. On mountain slopes and in highly dissected country, soils are immature, usually deep and always well drained. These are essentially forest soils. On flatter ground, unless the soil-forming material consists of nothing but pure quartz sand as in the caa-tingas, ground-water soils develop, first with an impeded, mottled horizon, later with an iron pan also. Drainage conditions worsen to the point where forest must give way to savanna. Later the flat, ill-drained savanna site may be dissected by a new erosion cycle and if not totally destroyed may come to form a new, more or less flat or gently sloping surface with the topsoil gone and remnants of the broken iron oxide horizon left strewn as fragments on top of the mottled clay horizon. Thus the savannas we see are of two types, the one "sandy," on flat expanses with sand-over-clay or sand-over-ironstone soil, the other "stony" on relatively elevated ground with clay-with-ironstone soil. The forest lands are on recent alluvia where soil formation has as yet scarcely begun, on

mountain or hill slopes, or on young plains where soil drainage has not yet developed too unfavorably. Gallery forests, be it noted, although they occur in savannas, must be classed as young sites, situated on the steep slope of a ravine or a strip of recent alluvium. It is quite wrong to assume, as Bouillenne did, that the same soil underlies both the gallery forest and the savanna. It cannot possibly do so.

The occurrence of savannas on the lower Amazon and in the delta, not on the upper Amazon, is fortuitous and is not to be related to climatic factors. The savannas in the delta lie in a very wet region. The fortuitous circumstance is just that the lower Amazon and delta happen to contain the necessary sites of sufficient topographic maturity. In the upper Amazon basin the terra firme is presumably a very highly dissected peneplain of very small relief like the south of Trinidad with only immature soils on the short steep slopes.

The caa-tingas and campinas are associated with deep, white quartz sand deposits derived, not necessarily *in situ,* from granite. Consisting of little but inert quartz, this material is unable to form a ground-water laterite and remains freely permeable. It constitutes a medium excessively freely drained and of very high acidity, so that moisture is consistently of low availability. The vegetation is thus of the "dry evergreen" or sclerophyll type. There is presumably a better moisture supply in the caatinga than in the campina, due largely to greater depth of the sand.

SUMMARY

1. The savanna is a plant-formation of tropical America comprising a virtually continuous, ecologically dominant stratum of more or less xeromorphic herbs, of which grasses and sedges are the principal components, with scattered shrubs, trees or palms sometimes present.

2. Three sub-formations can be recognized: Tall bunch-grass savanna, short bunch-grass savanna and sedge savanna. The tall bunch-grass savanna can be further subdivided into four phases—open, orchard, palm and pine savannas.

3. Tall bunch-grass savanna is composed of perennial, xeromorphic grasses up to 3 ft. in height, disposed in clumps and associated with many sedges and other herbs. Open savanna is treeless; orchard savanna includes scattered gnarled trees and shrubs; palm savanna, palms; and pine savanna, pine trees.

4. Short bunch-grass savanna is composed of xeromorphic grasses up to only 1 ft. in height, disposed in clumps. Thorny trees may be present.

5. Sedge savanna is composed of relatively xeromorphic sedges up to 18 in. in height, not tufted, and associated with many small moisture loving ground plants such as bladder-worts, ferns and mosses. Small evergreen trees and shrubs may be present.

6. Savannas occur under a great variety of climatic conditions from annual rainfall of 20 in. with seven or more drought months up to over 100 in. with negligible drought periods. Short bunch-grass savanna tends to predominate where there are less than 35 in. annually and sedge savanna with over 80 in.

7. All types of climate in lowland tropical America, given favorable site conditions, are adequate to support woody growth of some kind. A tropical grassland climate does not exist.

8. Savannas occur upon ill-drained country of little relief, most generally a senile landscape such as an old alluvial plain or a reduced upland.

9. All types of savanna may be swept by regular fires and the vegetation is so adapted as to be fire resistant. The herbaceous vegetation does not, however, depend upon fire for its maintenance and the savanna is an edaphic climax, i.e., it is determined by soil and site conditions.

10. Natural drainage is the most important characteristic of tropical soils affecting distribution of vegetation and chemical status is of little account.

11. The natural drainage of savanna soils is affected unfavorably by the lack of relief and the internal physical structure. Usually savanna soils exhibit the superposition of a permeable horizon upon an impermeable, or are extremely compact and impermeable throughout the profile, so that no true water table exists.

12. Savanna may be characterized as the vegetation of the highly mature soils of senile land-forms (or, in some cases, of very juvenile sites) which are subject to unfavorable drainage conditions in the form of intermittent perched water tables, with alternating severe periods of waterlogging and desiccation.

13. The soils of upland forests are well-drained, by virtue either of porosity or relief or both.

14. Specialized swamp forests occur on ground subject to flooding, but the site differs from savanna in that a normal water table must be present.

15. Temperate grasslands, for which the term "steppe" should be used, also represent a habitat almost perpetually adverse to growth, but the causes are climatic.

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